THE ANDEAN CONDOR:
A FIELD STUDY

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Author's Preface

When I was pursuing condors in the field a quarter century ago, the object was simple: to see as much as I could all that condors did and, from that station, make as much sense as possible about their lives, their past, their future. After two years in the field and another four to five years of research and writing, I had a manuscript in hand that I wanted to see published. That goal proved as elusive an odyssey as that of chasing after high-flying condors in the roadless Andes. Both the University of Chicago Press and the University of California Press wanted the study presented in terms of a theme, a single topic, something perhaps along the line of 'the biodynamics of scavenging.' But as I relate in the introduction, the work has always seemed to me more valuable as a normative study rather than a thematic one. In the services of both the bird and science, good baseline data become more valuable with each passing day.

A near miss at publication followed when the Museum of Vertebrate Zoology in Santa Barbara put together a proposal for a series of books in which the condor work would lead off. But, as I would not accept an ultimatum to delete a chapter and half the tables, we swiftly achieved an undone deal. I do understand their misgivings for the data presented there (too patchy for any meaningful statistical analysis); nevertheless I deem those survey records invaluable as a snapshot for coastline dynamics among scavengers at that time.

I know how presumptuous I have seemed and have been in demanding publication of an unwieldy tome where the only theme is the organism itself: a dry, statistics-laden text clogged with scores of tables and figures.

I did not go to South America with an armload of hypotheses, nor did I ever perform any tests. I was a watcher. I took whatever the condor was willing to provide. It was a life-history study, and I was sensitive to the criticism of 'woodsy-loresy.' But I wanted to know more about

condors and do what I could to slow their imminent waning. Moreover, I loved the bird, and I loved living where it lived. To that end, I knew from my days in the library which pursuits were useful and which were not. I am glad to say that those considerations remained the ultimate landmarks throughout a long confusion of vanities and ambition, that and my good luck in this alliance with The Craighead Wildlife-Wildlands Institute (with the help of Derek Craighead, who now leads Craighead Beringia South), a foundation that holds similar views about what it is worth knowing.

This note from my journal in the early days of work seems appropriate here:

A lone condor came first, then two together, another single bird, and finally another pair followed. Six adults drifted beneath in the canyon, wheeled silently in and out of the black morning shadows. With this first real chance I had to observe a condor in close quarters, I scribbled furiously, desperate to catch every detail of the spectacle. But it wouldn't work. I could not sustain that posture of the detached observer. The loveliness of it all overwhelmed me.

On that morning in Colombia, after having spent every daylight hour of five weeks hidden in a blind, after having killed five horses, after having failed to attract anything but black vultures, after having discovered that morning that a sixth horse had been dragged over the rim—probably by a mountain lion—and had fallen a half kilometer toward the river below, after all that, not one condor came to see, nor two, but six. I put the notebook down and watched.

Jerry McGahan, August 17, 1993

Eighteen years later, I revisited this study on the computer to find I could not open any of the files for the tables. The software used to prepare them was unknown and out-of-date. After some searching and some discussion with others, Jay Sumner and John W. Craighead among them, I undertook (with considerable help from Jay) to get the manuscript updated so that others can peruse it at will on the internet. This project involved copying the galleys for the hand-

edited tables as photos and making my corrections on Photoshop. I also edited the text. Jay helped me get the tables, figures, and plates on photo files. If you are reading this, I am a happy guy.

Jerry McGahan, September through November 2011

Acknowledgments

This work—the planning, preparation, the field study itself and the subsequent analysis, editing, revising, and publication—spans four decades. It represents a culmination of effort by many people. For their help and collaboration, I am profoundly grateful.

Of this group, Libby Sale, my former wife, was the most important. She gathered part of the data, took the photographs, and helped prepare the manuscript. To smooth the flow of the text, I often use the pronoun 'I.' Many of the field observations would be more accurately described from the point of view of 'we.' In this conceit of uniformity, her contribution has been slighted, along with that of several others who worked with me in the field.

In planning and organizing the study, I received important information and advice (with encouragement) from Maria Koepcke, I.R. Brimwood, N. Philip Ashmole, Alexander Wetmore, William Vogt, R.C. Murphy, Carl B. Koford, Enrique Avila, Dean Amadon, William H. Phelps, Tony and Marion Morrison, Hans Dossenbach, and Jay Schnell.

In problems with equipment and logistics, I was assisted by Teresa Nealon, Walter Holthaus, Kenneth Olesen, Frank Iwen, Craig MacFarland, Charles Stearns, Heinz Lettau, Donald Chandler, David Barash, Tom Grubb, and Hal Mahan.

In Colombia, Gerardo Luna kindly allowed us to live at his finca, Sal si puedes, for a year. Carlos Lehmann V and the staff of the Museo Departamental de Historia Natural in Cali were frequent and gracious hosts. Carlos established a base of study for us and saw to it that we

got there with all our equipment, a major accomplishment. William Millie of Chile and Rodolfo Scaiola of Argentina guided me to various study areas and each shared with me knowledge of their country and its fauna. Dr. Ramon Ferreyra and Dr. Oscar Tovar of the Museo de Historia Natural provided us with lodging when we were in Lima, Peru. Carlos Ponce del Prado has been instrumental in seeing that study results have been used in managing the condor in Peru.

The following people contributed many hours chasing condors with us: Karen Craighead, Miguel Pinta, Luis Pinta, Jay Sumner, Daniel Anderson, and Maximileno Ormeño. Providing a number of important suggestions, Joseph Hickey assisted and advised us in the field.

Methods of analysis used and interpretations of the results were often end products of editorial assistance and conversations with Jack Hailman, John Neess, Vance Tucker, Allen Barduhn, John Magnuson, David Thompson, Daniel Smith, and Betsy Brauer. Gordon Stephenson helped with many analyses and solved an important geometric conundrum when I lost a gauge used in studying condor flight. Figures in the text were done by John Dallman and Cheryle Hughes. Jodie Peirce assisted in data reduction and in the preparation of the manuscript. Jan MacFarland, Tibber Sindt, and Noel Weaver typed the manuscript on a word processor and suggested revisions. Janet and Jordan McGahan and Simon and Duncan Crawford also contributed clerical services. Filming efforts would have failed without the help of David Arnold and Joanne Hess.

Dr. John Emlen helped in planning the study and in securing the finances required. His editorial assistance on the final manuscript was invaluable. Roland Clement helped obtain funds to assure final analysis and preparation of the first draft. Colin Pennycuick, Deborah Davis, Sanford Wilbur, David Houston, and Patricia Parker provided revision suggestions and other editorial help. At the Craighead Wildlife-Wildlands Institute, I got help from John J. Craighead, Derek Craighead, and John W. Craighead in assembling a finished copy of the manuscript

The investigation was supported by a grant (GB-19449) from the National Science Foundation and a fellowship from the Danforth Foundation. The National Geographic Society provided film for still and moving pictures. The University of Wisconsin furnished most of the equipment; three chapters of this work constituted a Ph.D. thesis for that institution. Grants from the U.S. Bureau of Sport Fisheries and Wildlife (as administered by the National Audubon Society) and the U.S. Section of the International Council for Bird Preservation funded final preparation of the study.

In the fall of 2011, Jay Sumner and David Rockwell worked hard to get the manuscript with all its tables, figures, and plates into this final pdf file; and Janet McGahan put in another round of proofing. Thank you for that.

CHAPTER 1. THE STUDY

INTRODUCTION

In my library review, I was fascinated by the extremes of existence characteristic of the Andean condors.[1] These included the extended range and wide divergence of habitats, its own large size, and the exclusive role it played in past and present cultures of some Andean peoples.

The bird is exceeded in weight by a small number of other flying birds, including some bustards, storks, and swans, and in wingspan by only a few species, mostly albatrosses (Fisher and Peterson, 1964). With the exception of the California condor, no other vultures, neither New nor Old World species, attain on an average basis the size or weight of the Andean condor. This immense scavenger has in recent times ranged the entire length of the Andean chain and beyond, a distance over 7000 km^2, where it frequents a spectrum of habitats that extend from barren glaciers in the high alpine zones down to virtually sterile wastes of the Atacama desert. Today condors still live in the mountains of the Sierra Nevada de Santa Marta 11° north of equator and in scattered areas of the stark islands of Tierra del Fuego 54° south of the equator, wet and treeless equatorial páramos of Colombia and Ecuador, coastal deserts of Peru and Chile, vast altiplanos of Bolivia and Peru, and into the pampas of Argentina north to the Rio Negro, a remarkable range of habitats for a bird that would seem to have tremendous problems of movement because of its large size.

The extent to which some native people identify with the condor is extraordinary. Not only have condors figured as artistic motifs in weavings, ceramics, and sculpture, or as characters in folklore and myths of creation, but some natives believe the fate of this bird parallels their own. In several different Andean fiestas live condors have been used in rituals that may be symbolic of the Spanish conquest and its aftermath.

For centuries, the condor entranced newcomers, too, scientists and explorers, Charles Darwin and Alexander von Humboldt among them. At the turn of the nineteenth century, Humboldt collected specimens and recorded techniques used by native people for trapping them. On his famous climb of Chimborazo, he observed and noted condors flying at altitudes of 4900 m. Darwin (1845 pp. 213-214), with characteristic perception, recorded observations not only on the habits of the condor but examined aspects of flight in some detail.

> "When the condors are wheeling in a flock round and round any spot, their flight is beautiful. Except when rising from the ground, I do not recollect ever having seen one of these birds flap its wings. Near Lima, I watched several for nearly half an hour, without once taking off my eyes: they moved in large curves, sweeping circles, descending and ascending without giving a single flap. As they glided close over my head, I intently watched from an oblique position the outlines of the separate and great terminal feathers of each wing; and these separate feathers, if there had been the least vibratory movement, would have appeared as if blended together; but they were seen distinct against the blue sky. The head and neck were moved frequently, and apparently with force; and the extended wings seemed to form the fulcrum on which the movements of the neck, body, and tail acted. If the bird wished to descend, the wings were for a moment collapsed; and when again expanded with an altered inclination, the momentum gained by rapid descent seemed to urge the bird upward with the even and steady movement of a paper kite. In the case of any bird <u>soaring</u>, its motion must be sufficiently rapid, so that the action of the inclined surface of its body on the atmosphere may counterbalance its gravity. The force to keep up the momentum of a body moving in a horizontal plane in the air (in which there is so little friction) cannot be great, and this force is all that is wanted. The movement of the neck and body of the condor, we must suppose, is sufficient for this. However this may be, it is truly wonderful and beautiful to see so great a bird, hour after hour, without any apparent exertion, wheeling and gliding over mountain and river."

He performed an experiment on the condor's sense of smell.

> "I tried . . . the following experiment: the condors were tied, each by a rope, in a long rope at the bottom of a wall; and having folded up a piece of meat in white paper, I walked backward and forward, carrying it in my hand at the distance of about three yards from them, but no notice whatever was taken. I then threw it on the ground, within one yard of an old male bird; he looked at it for a moment with attention, but then regarded it no more. With a stick I pushed it closer and closer, until at last he touched it with his beak; the paper was then instantly torn off with fury, and, at the same moment, every bird in the long row began struggling and

> flapping its wings. Under the same circumstances, it would have been quite impossible to have deceived a dog."

And finally he noted a number of interesting relations between condors and people, among them the techniques of trapping.

> "The Chileños destroy and catch numbers. Two methods are used; one is to place a carcass on a level piece of ground within an inclosure of sticks with an opening, and, when the condors are gorged, to gallop up on horseback to the entrance and thus inclose them: for when this bird has not space to run, it cannot give its body sufficient momentum to rise from the ground. The second method is to mark the trees in which, frequently to the number of five or six together, they roost, and then at night to climb and noose them. They are such heavy sleepers, as I have myself witnessed, that this is not a difficult task.

Early anatomists, also intrigued by the giant bird, searched for characteristic peculiarities (Harlan 1830 ; Beddard 1890, 1902, 1904). Later Fisher (1942, 1944, 1946) analyzed in detail skeletal, muscular, and feather-tract structures of the Andean condor and other cathartids. Yet in the field, little work on the life history followed those first records by Darwin and Humboldt. In this century a few naturalists assembled scattered observations with anecdotal data from other sources, like zoos, and from them fit together rough assessments of how the condor lives in its native habitat (Apolinar, 1914 ; Housse, 1940 ; Lehmann, 1940 ; Goodall *et al*., 1951 ; Olivares, 1963). Aside from some short notes describing encounters with wild Andean condors (Adams, 1907 ; Castellanos, 1923,1928; Murphy, 1925, 1936; Vogt, 1941; Wiggins, 1945; Koford, 1957) most of the documented data on the condor come from zoos and describe the maintenance and reproductive behavior and plumage changes with age of captive birds (Beebe, 1909; Onelli, 1910; Janda, 1938; Portielje, 1949; Dathe, 1952; Lint, 1959, 1960; Poulsen, 1963; Whitson and Whitson, 1969; Gailey and Bolwig, 1973). Recent attempts to learn more about the movements of wild condors using radio-tracking techniques met with little success because of technical problems (Fowler, 1969).

Alluring sketches of a majestic and looming backdrop laced the correspondence that I received from scientists and explorers familiar with places where condors flew. Alexander Wetmore, dean of American ornithology, described the northernmost range of the condor with pointed reverence. "The Sierra Nevada de Santa Marta is an isolated mountain chain in northeastern Colombia, separated widely from the Andes proper. In fact, it is quite an amazing place since the mountains rise to 19,000 ft. and slope toward the Caribbean coast where beyond the continental shelf there is a vast ocean deep that goes down to 5 miles before it hits bottom." A.W. Johnson, the venerable Chilean ornithologist, under the mistaken impression that I planned a census of the Andean condor, warned me with explicit eloquence. "I think you are planning to attempt the impossible. The normal habitat of the Condor is the highest reaches of the Andes, the steepest, most rugged and second highest mountain range in the world. It stretches for 5000 miles from Venezuela to Tierra del Fuego and, except for a very few places where jeep-roads have been built, the altitudes over 4000-5000 meters where the condors for the most part live, are accessible only by horse or mule. How could you possibly take a census under conditions where a condor may range in an hour farther than a man could possibly follow him in a month? As for examining the nests, these are usually on such tremendous cliffs that only about 1 in 10 can be reached even with ropes."

These descriptions and admonitions had not been overstated. Every place where we saw condors was characterized by some extreme of climate or topography. Before choosing as areas of study a deep canyon of equatorial Colombia, an austere badlands of broken rock in northern Peru, and a desert shoreline—also in Peru—that was both profoundly devoid of and abundant with life, I visited other potential sites in the western half of the continent: high-altitude <u>páramos</u> in Colombia and Ecuador, the altiplano and sierra of Peru and Bolivia, and sea cliffs in northern Chile. William Millie guided me on an extended trip through the desert lowland hills of central

Chile, and Rudolfo Scaiola arranged a pack-trip on mules through part of the pre-Cordillera range near Mendoza, Argentina beneath the shadow of Aconcagua, highest peak in the Americas. Although condors were present in every area, the sites in this investigation were chosen on the basis of divergent habitats, on the likelihood of locating nests and observing condors from day to day, and on conditions favorable for either attracting or following the large birds.

The initial questions posed for this study dealt with the problems of mobility and adaptations to the different habitats and how they relate with competitive species. For example, condors would seem to be critically dependent on wind conditions for flight, so how do they satisfy all the biological requirements for life and reproduction in such a wide variety of climates and topography? Are they as dependent on air conditions as previously supposed? Are they indeed less mobile than the other smaller New World vultures they live among? How do the different avian scavenger species compete for carrion without excluding one another? Do condors have special adaptations for handling extremes of ambient temperature?

In this project, as with most field studies, the patterns of analysis and some of the questions asked changed when the study moved from desk to field. We discovered at once that the chief obstacle to a successful study was simply that of finding and observing a wary bird with such great powers of movement. One assumption proven false was that all basic life-history data would accumulate during the pursuit of these more specific questions. We never were able to locate a nest in the early stages of incubation and brooding: such data for wild-living Andean condors are yet to be recorded. As originally intended, however, flight of the condor was analyzed in detail with an eye to both biophysics of flight and its implications for behavior and ecology of the big scavenger. The linear distribution of food on the Peruvian coast presented an excellent opportunity to analyze in detail the relations of a condor population to its food supply and to other avian scavenger populations.

Several other major portions of this study were not envisioned until after field work began. The subject of any animal field study often "tells" the investigator which facets of its life will divulge information and those that will not. When condors were not foraging, they often perched for long periods on cliffs visible from our observation posts. Extended periods of observation on these birds permitted us to gather considerable data on postures, body maintenance, and weather-related behavior. The quantity of data gathered allowed us to make stochastical analyses of maintenance behavior and to describe the diurnal variation in the use of some patterns.

In three different study areas, condors frequented our baits in groups so that we were able to amass large amounts of information on social behavior and on their relations with other species, as well as on feeding behavior. We found that some Andean condor pairs engaged in sexual activity at a comparatively high level whether they were nesting or not. This situation and the opportunity to view several nests for extended periods permitted a detailed study of many aspects of condor reproduction in nature. In Peru, we visited a number of the fiestas involving condors and recorded information on the bird's role in the lives of these people and those before them.

Basically, then, the book is organized according to these topics, each representing a major chapter. The study did not pursue a single major question, but exploited instead the opportunities outlined above. For this reason a separate section on methods does not appear; methods employed in each investigation are presented in the chapter dealing with that subject.

The general aim of this study is to present in modern terms a life-history study of the Andean condor. The investigation employs contemporary techniques in the analyses of behavior and ecology. Specific objectives are as follows: to describe simple behavior patterns and postures and determine their functions; to describe the formation and maintenance of pair bonds

and the organization of reproductive activities among parents and young; to isolate characteristic social relations among condors of different sex-and-age classes, migratory status, and populations and to isolate basic principles of social structure; to describe interspecific relations, relating variation for different species and localities to ecological factors; to describe feeding behavior of condors and other avian scavengers and determine food relations among competing species; to gain an understanding of how condors fly; to describe mortality factors; and, finally, to survey how condors have influenced various South American cultures.

The analysis is inclined heavily toward quantification and methodology. In this age when both habitat and the populations of the birds themselves are undergoing changes of extraordinary magnitude and fleetness, it is essential to record, in the "instant" of a study, data of a physical description that are objective and unambiguous. The ultimate use for such information is twofold: to establish baseline data for a threatened species and to address scientific questions of function and origin. Good information for the second objective is increasingly rare and elusive for wild-living organisms in natural settings (that is, in areas where the animal encounters conditions like those in which it evolved, where artifacts and "improper" responses are least likely. The data we gathered is of use to the extent we are precise about what we saw and measured. In the study of flight, an objective approach was both obvious and straightforward, an exercise in biophysics; in the analysis of social behavior, a clear objective was more difficult to maintain. For the latter, I had to sift through abstraction to explore the meaning of various actions. The subject of social behavior was the most difficult to analyze, and that chapter the most formidable to prepare. We amassed much data on the smallest motions. Some may question the value of discriminating behavior patterns to such fine degree. Why, for example, must one consider whether or not a condor supplanted from a feeding site moves away immediately or waits 5 or more seconds? Is this an example of trivial quantification? Yet, close

attention to these details is warranted if the outcome of an interaction between two condors seems to depend on the presence or absence of these more subtle differences. We found, in fact, that a supplanted condor generally hesitates (for 5 seconds or longer) before departing when dominance-subordinance relations between the two are not explicit.

To make both a significant and a lasting contribution to the understanding of the social behavior of the condor one must carefully discriminate among the different behavior patterns and record frequencies of the pattern in various contexts. In this way, meaningful comparisons can be made both with contemporary data from studies of other species and with data obtained in the future. Additionally, as new concepts and theories of social behavior appear, data objectively collected and presented can be re-examined for new interpretations. Hence, in this study of social behavior, the patterns are first observed and recorded according to their physical appearance; then the subjects of function or social effects are considered. For example, one series of patterns used by condors supplanting other birds from a feeding site are designated and recorded as peck/jump patterns. When relations between different sex-and-age-class birds are considered, the frequency of the peck/jump approaches are used as a gauge of aggressiveness. Aggressiveness, then, is a more subjective term, but represents an essential concept in forming general statements about why certain condors behave with one another as they do. Thus, data recorded in the field are presented, usually in tabular form, so that a reader can visualize what we saw and determine how often we saw it and in what context. Subjective judgments about whether a certain movement is aggressive are reserved for summary and discussion sections dealing with the social function. This manner of presentation applies to other subjects as well; so, for example, under the behavior pattern of sunning, a subheading for description precedes that of function.

This investigation begins and ends with the same subject of man and condor, where I

examine first the influence condors have had upon man and ending with the more gloomy aspects of the reverse condition. The final sections are the most timely, for if current trends continue, future investigations of the condor may be confined to the zoo. The birds are wary and may nest only in remote areas, an ever diminishing resource in all of Latin America. Although condors are extremely cautious about alighting within sight of man, they rarely fail to examine closely from the air any human presence that is relatively new for an area. Thus, guns represent an extraordinary deadliness for this target that seems as impulsively curious as it is large. In addition, new evidence indicates that pesticides might be eliminating them with insidious silence by halting reproduction.

Empty skies bear a speciously benign testament to that passing. "Yes, there were condors here," many told us, pointing at a bluff or mountain or canyon rim, "but they have left now. They have not returned." Highway construction in our Colombia study area has added even that region to the tally of lost refuges. Gerardo Luna Delgado, whose *finca* was generously given to our use during the Colombian phase, recorded that passing with expressive regret, *". . . desgraciadamente se exterminaron la construcción de la nueva carretera acabó con toda esta especie, tan bella y admirada por todo el mundo . . . Esta pagina tan bella de otros tiempos, desgraciadamente pasó a la Historia." [Unfortunately by the time they finished construction of the new highway, it was over for [the condor, a bird] so beautiful and so admired by all…in the course of history, that lovely page of other times is gone."*

It is likely that condors will never be driven to extinction, that these tractable and easily bred animals will always be available for captive display. That would be the most insignificant of consolations. Without recourse to wild-living condors, biologists will have lost the most incredible representative of the giant avian scavengers, while anthropologists and archaeologists will have lost another key for interpreting the dreams and experience of another time, another

world and culture—these all irretrievable links with the past. Beyond this, everyone has lost a bond to that vague and ineffable part of our own spirit, a part in everyone that must stir when a wild-living condor soars just overhead, when *el condor pasa*.

> . . . and when the oldest men of the clan take the king of birds, garlanded with the heraldic ribbons of the Empire and the Republic, and throw him into space with a hayllis! of joy they are not carrying out a simple folkloric ritual, they are symbolizing graphically the immortality of the Empire and the race, for legend says that as long as condors range the skies, the gods will find their way back.
>
> Hernan Velarde[3]

STUDY AREAS

Colombia

The Colombia study area is in the Department of Nariño about 25 km west of the city of Pasto. Approximately 170 sq km in size, the area includes the confluence of the Rio Pasto and the Rio Juanambu (Figures 1,2). A rolling plain in the center of the area is bounded by these two immense river canyons. Escarpments fall one after the other down winding green walls that descend over 600m in some places (Plate 1). A smaller gorge, known locally as the Quebrada Santana, runs into the Rio Pasto canyon near the Pasto Airport. Another gorge, similar both in size and configuration to the Quebrada Santana, enters the Rio Juanambu on the eastern side of the study area. This gorge, the Quebrada de la Toma, or Quebrada Cimaronas, runs parallel with the Rio Pasto and like the other canyons is a series of precipitous meadows and vertical rock faces with a stream at the bottom. Water in the two Quebradas form a series of pools, waterfalls, and cascades, whereas rivers in the major canyons exist predominantly as rapids. (Figures 1, 2)

Trees are few; some grow at the edge of the rivers and streams and in the bottoms of a few isolated gullies. Common shrubs that grow in open stands are *Lantana* sp., *Croton* sp.,

Figure 1. Locations of the three study areas. Colombia area, top arrow; Cerro Illescas, center arrow; and Paracas, bottom arrow.

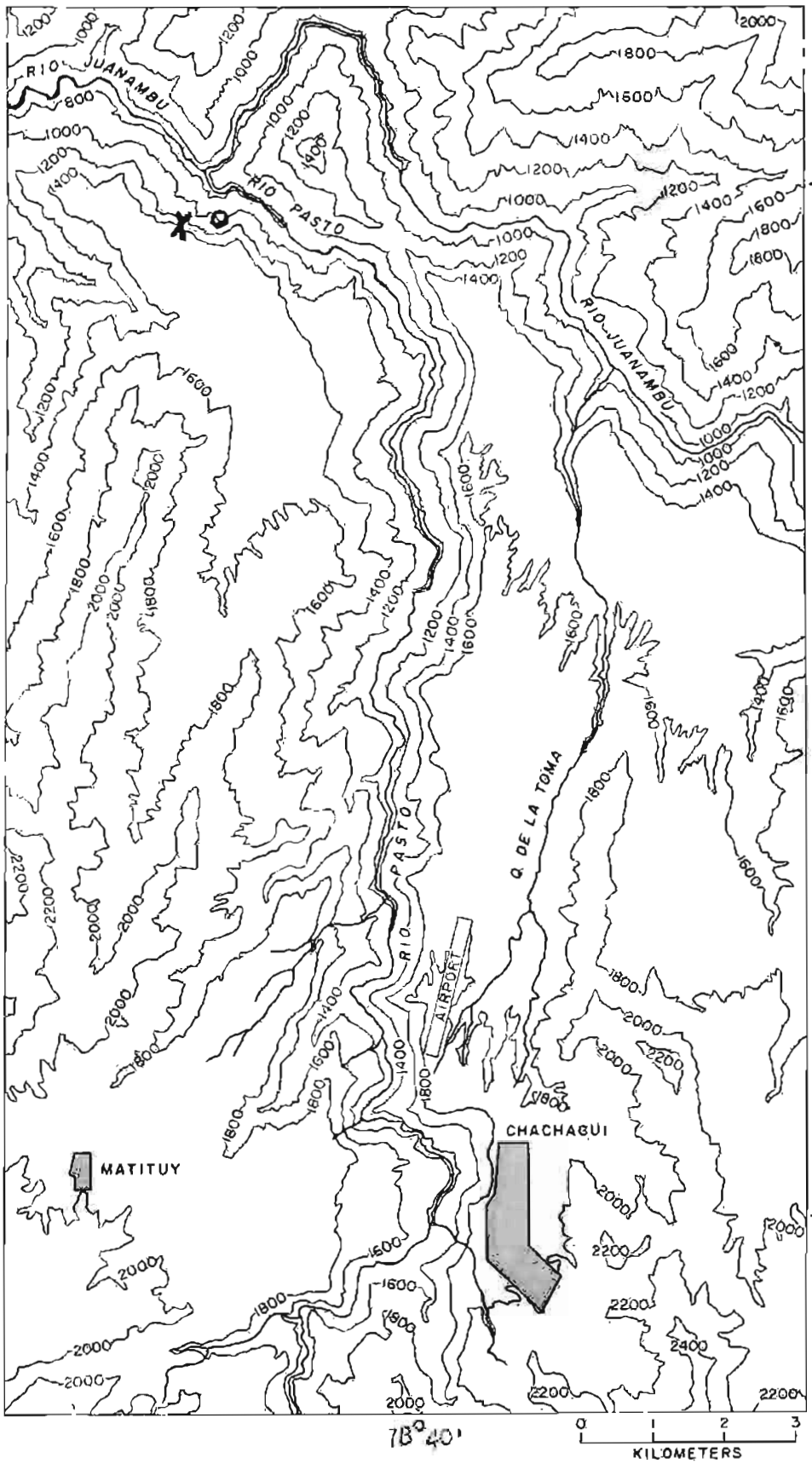


Figure 2. Colombia study area. The area is located 25 km west of Pasto in the Department of Narino. Elevation is in meters. X designates nest and roost area of pair 1, and O designates roost area of pair 2. The map is from the Instituto Geografico *Agustin Codazzi* in Bogota.

Plate 1. Colombia study area. The Rio Pasto Canyon near the center of the study area. Miguel Pinta was one of our guides. We lived with the Pinta family.

Cassia sp., and *Zexmania* sp. with the *Croton* predominant on the rim and plateau and *Lantana* near the bottom of the canyons. Grasses in the area include *Eragrostis* sp., *Setaria* sp., *Andropogon sensu latu*, and *Melinus minutiflora*; they grow luxuriantly on the steep slopes of the canyon but are more sparse in grazed sections.

Grazing by cattle has affected the vegetation of the area tremendously. On the central plain, grasses exist only as stubble in both wet and dry seasons. Cattle avoid taking the shrub *Croton*, so great stands of it cover much of the plateau, particularly the sides of small gullies and ravines that the cattle can reach. A few stands of large cactus dot the landscape. In the bottom of the two major canyons in areas where cattle feed, *Lantana* is the most important plant. Both *Croton* and *Lantana* grow well on hard and dry, eroded soil of this area. Enclaves of vegetation natural to this area exist only on the precipitous slopes of the canyon. Whereas bottomland in the canyons and the plateaus support scanty cover for a few species of shrub on barren and rocky soil, the canyon walls represent a verdant refuge for grasses. Tall grasses dotted with bromeliads grow in thick profusion on nearly vertical sites amid escarpments of stone. The only human effect on these preserves seems to be the fires that sometimes blacken part of the canyon walls during the dry season.

Skies of the study area are sunny and temperatures warm, usually ranging from 15^{o} to 30^{o} C. Rainy weather is more common during the two annual wet seasons that extend from April through June and October through December. Mean annual rainfall recorded at the airport is 72 cm (28.4 in). Typically, dry seasons bring higher temperatures and strong winds.

The study area includes two villages and an airport in the southern part of the study area. In the northern half of the area where most of the investigation occurred, the number of human residents probably numbered around 100. These people live a peasant existence, many of them caretakers for land owned by people living in Pasto. They care for horses and cattle, a few of

which are their own, and grow their own crops of corn, beans, manioc, and sugar cane on small level plots granted to them by the landowners for that purpose. In some instances, crops are grown on parts of the canyon wall too precipitous for cattle to graze. Almost all cultivated land is hand-tilled. Not all areas in the bottoms of the canyons are accessible for grazing. Those suitable are marked by switchback trails cutting their sharp zig-zag marks on the canyon walls. Few people live in the canyon bottomland, because level areas suitable for cultivation are so few.

I estimated that 14 different condors frequented this study area during the period of study; four adult males, four adult females, four immature males, and two immature females. The four adult males in the Colombia area were designated as AM1, AM2, AM3, and AM4: three immature males (IM1, IM2, IM3) and two immature females (IF1, IF2) were identified individually as well. I was unable to distinguish the four adult females one from another when perched but two of them, mates of identified males, could be recognized in the air by molting patterns in flight feathers. AM1 and his mate, AF1, a non-nesting pair that mated, foraged and roosted together, were designated as pair 1, and AM2 and AF2, a nesting pair, were designated as pair 2. Roosting in the same locality, each pair used a separate set of cliff ledges for night perches referred to here as roost areas 1 and 2, respectively (Figure 2). During part of this early observation period, another pair roosted in the same 1-sq-km area, just out of sight of our observation point. We were unable to identify these birds individually. One other pair of adults, a nesting pair, observed here during the latter part of the study, may have included members of either pair 1 or 2; these birds are referred to as AMA and AFA of pair A.

We worked in this area from June 1968 to March 1969 and from March 1970 to June 1970. Shortly after we finished our work in 1970, construction began on a new section of the Pan-American Highway that cut through the center of the study area as it crossed the plateau from the airport to a bridge near the confluence of the two rivers. The condors left and probably

will not return.

Cerro Illescas

The north coast study area of Peru encompassed a small range of desert mountains, the Cerro Illescas (Figures 1, 3). About 30 km by 15 km in size, this range lies on an isolated desert peninsula halfway between the cities of Chiclayo and Piura. The hills and ridges are austere projections of broken rock that support very little vegetation (Plate 2). The highest points in these badlands do not exceed 450 m. Most of the sedimentary formations in the range are from the Paleozoic and Tertiary periods; intrusions of igneous rock in the southern part are from Cretaceous and Paleocene times.[4] Two large, dry stream beds, Quebrada La Montera and Quebrada Nac move in opposite directions from the center of the range, east and west, respectively. Except for level beds of gravel in the few larger ravines, most of the land lies in a steep relief of gullies and ridges. I found two saline pools in the range, one in Quebrada Nac and another in an unnamed gully on the east edge of the range. Fresh water streams or pools apparently do not exist in the area except, perhaps, during the years when a peculiar weather anomaly called *El Niño* brings rain to Peru's desert coast (Figure 3).

In most of the range, only a few shrubs or trees dot the hills of rock. Low clouds from the sea carry a misty precipitation that supports some grasses on the southern part of the range, especially in the winter. This *lomas* vegetation helps support a feral goat and burro population, together with a few domestic goats run by a single goatherd. The largest and most common tree is a kind of mesquite, *Prosopis chilensis*. Pods from the tree also provide food for burros and goats. Two other small trees, *Capparis angulata* and *Parkinsonia aculeata*, are present, although *Capparis* usually grows as a shrub. Other shrubs include *Maytenus octogona*, *Capparis*

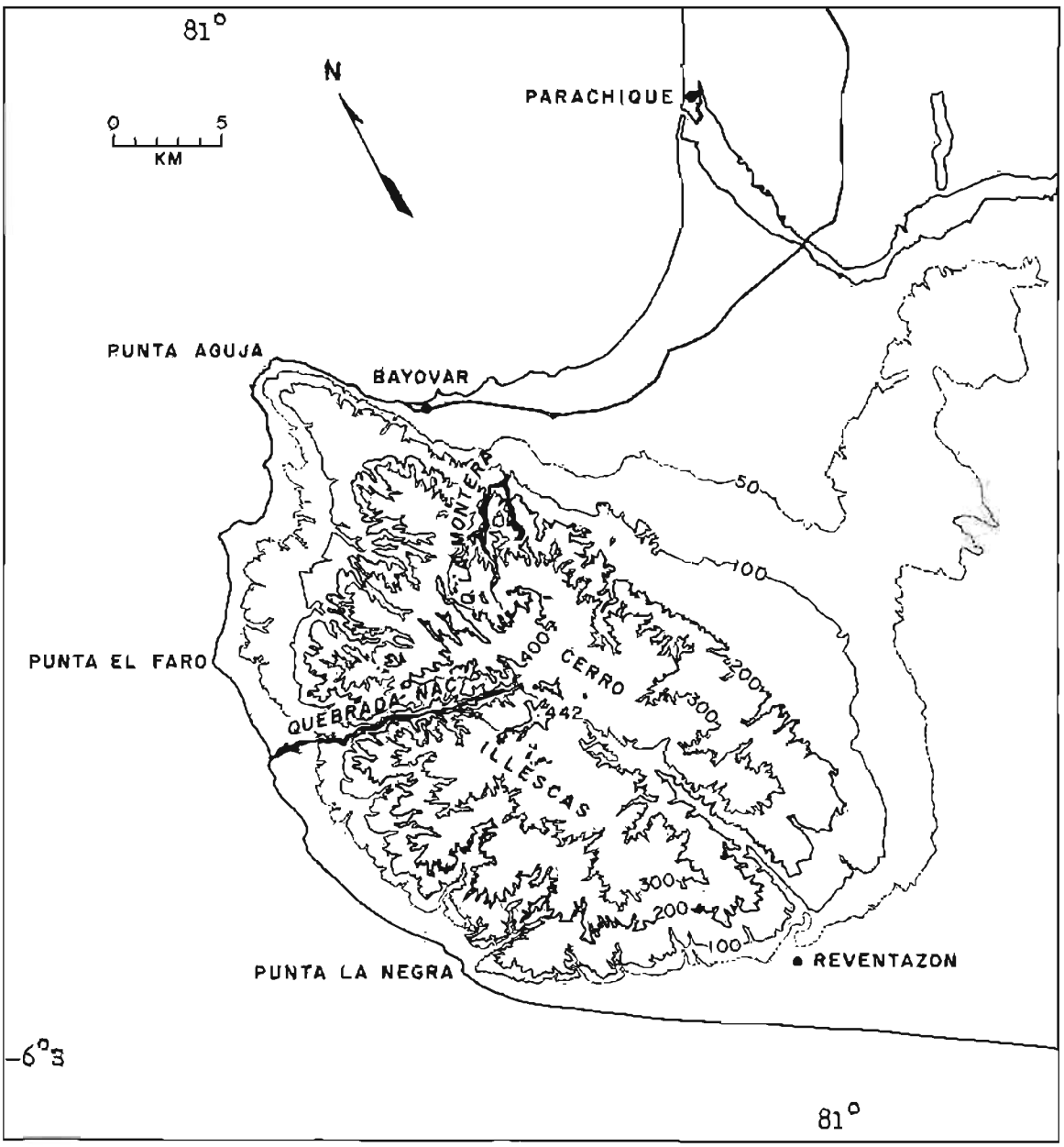


Fig. 3. Cerro Illescas study area located about halfway between Chiclayo and Piura, Peru. Altitude is in meters. Map is from Instituto Geografico Militar in Lima.

Plate 2. Cerro Illescas study area. A roost site for frigatebirds.

ovalifolia, and *Scipharia spicata*.

The climate in this area is hot and dry. Although the offshore waters of the Humboldt Current are cool, the strong south wind blowing off the ocean onto the south and central coasts of Peru is diminished at this latitude, so its cooling effect is absent. Reflectance of the sun's rays off sand and stone contribute to the heat, particularly on those days when little air is moving. Average temperatures are in the mid-twenties (C^{o}). Unlike the southern coast, this area has a few small and low cumulus clouds appear in the afternoon over the range. Except for the winter drizzle from low clouds, rainfall in this area is rare. The mean annual precipitation is 14 cm.

The mountain range itself is not inhabited by people. During our period of study, a lone goatherd lived at Reventazon and pastured his goats on the southern foothills of the range. Salt and phosphate are mined southeast of the range in the Sechura Desert, and a phosphate mine operates on the coast at Bayovar north of the mountains. Huts and sailboats stand in lines along the beach at Parachique, a fishing village north of the Cerro Illescas. Punta El Faro, on the western edge of the mountains, supports an unmanned lighthouse. Repairs are made on an annual basis by driving from Reventazon along the beach when the tide is out. An occasional donkey caravan travels from Sechura, a town 70 km north, to the foothills of the Cerro Illescas to collect firewood.

Because we logged fewer hours in the blinds here, we could not distinguish individual condors. Immature birds seemed to comprise about one third of the population. Few, if any, people visit these mountains, and the condors here were not as wary as in other places. They probably nested here. They fed on dead goats and burros and on sea lions and sea birds that washed up on the beach.

Paracas

The second study area in Peru is a 70-km strip of desert coastline just south of Pisco, a strip that includes the Paracas Peninsula (Figures 1,4). We worked in this area and in the Cerro Illescas from March 1969 to March 1970. The Paracas area is a rolling expanse of sand and stone almost completely devoid of vegetation. Three holophytic plant species, *Distichlis spicata*, *Sesuvium portulacastrum*, and *Salicornia sufruticosa*, grew sparingly on dunes near several beaches. I saw no other vegetation. The coastline is a series of rock faces and sandy beaches (Plates 3,4); sedimentary rock from the Paleozoic era stands along the sea in the northern part of the study area, whil the south features water-eroded formations with sedimentary rock formed in the more recent Quaternary period.[4] Rock faces are present only at the water's edge. Rolling hills and plains of sand, pebbles, and broken rock in patches of yellows, greys, and oranges are molded by the ever-present south wind into smooth oblong shapes, most of which lie parallel to the coastline. From the cost, we regularly observed one small island, Isla Zárate, during a period when condors and sea lions frequented its beaches and cliffs. Three coastal beaches censused on a regular basis during a food ecology study were designated as beaches A, B, and C (Figure 4).

Climate of this area is governed by the strong south wind blowing over the cold upwelling of water in the Humboldt Current. Although the desert is extremely dry, with precipitation rare except for some winter drizzle, temperatures are cool. Average temperatures remain in the lower twenties (C^{o}) and the mean annual precipitation is about 4 cm.

There are more people here than in the Cerro Illescas. The shacks of two fishing villages, Lagunillas in the north and Laguna Grande in the south, dot the beaches along the northern edge of several large bays. From boats with lines and nets, these fishermen take shark, bonito, mullet, cojinoba, and other fish, as well as an occasional porpoise, sea turtle, and penguin. From shore,

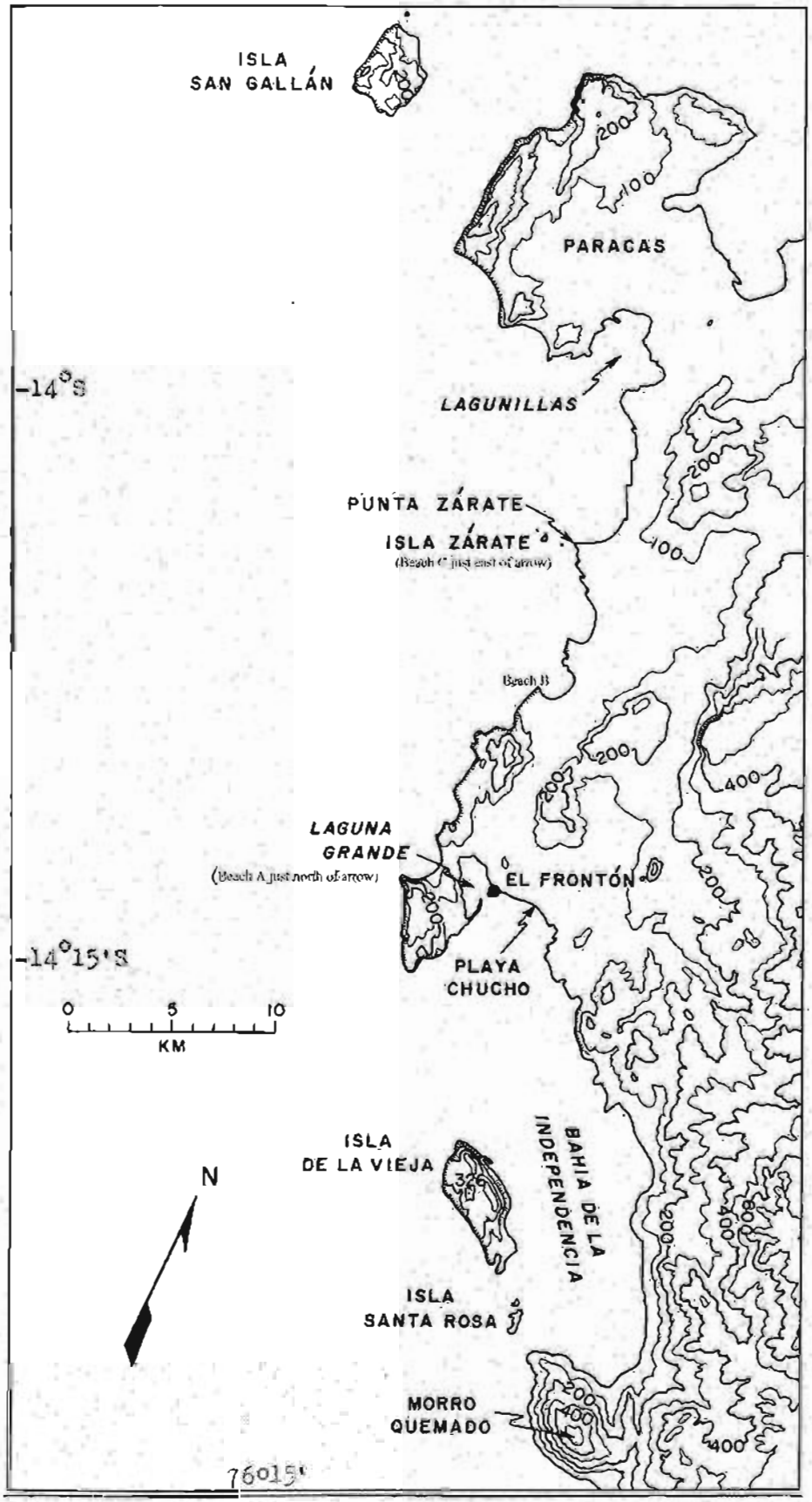


Fig. 4. Paracas study area located just south of Pisco, Peru. Map is from Instituto Geografico Militar in Lima.

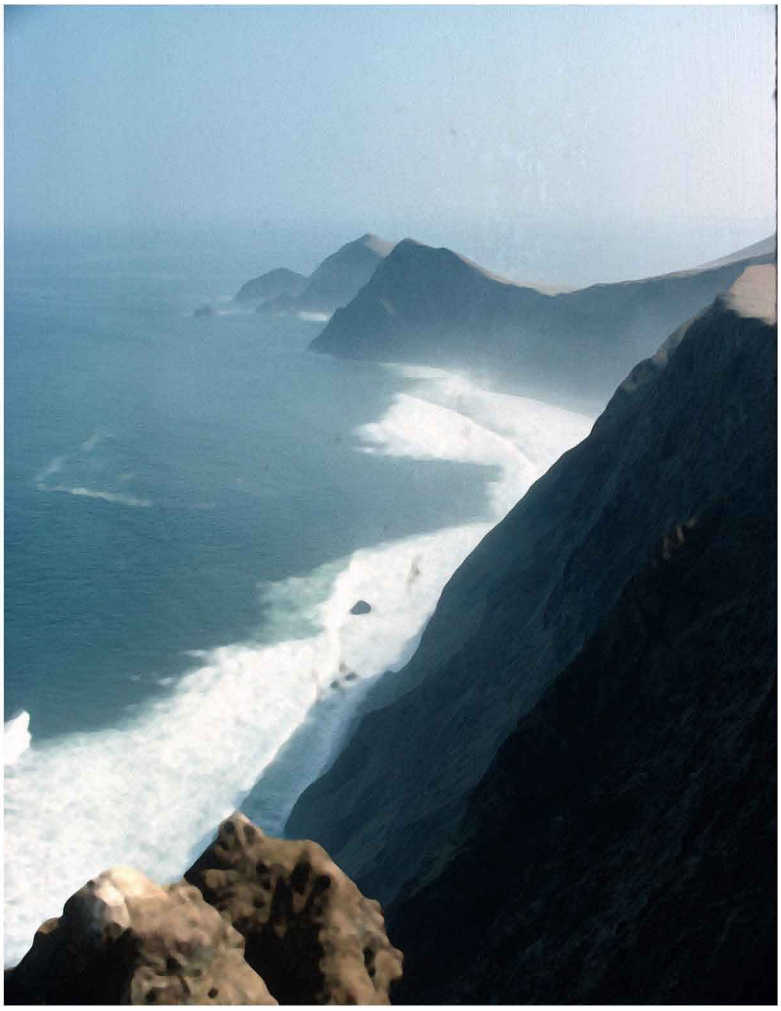


Plate 3. Paracas study area. A zone of coastal cliffs.

Plate 4. Paracas study area. All cliffs in this area are at the ocean's edge.

they take flounders, sea bass, and shark with lines and clams, crabs, and octopus by hand. These itinerant fishermen, as well as sport fishermen from Lima, visited all of the beaches frequented by condors in this study area. On six censuses of the condor population made during early morning hours, we saw from 2 to 30 people on these beaches.

All three study areas are in the time zone designated as Eastern Standard Time in the United States (+5 Greenwich Mean Astronomical Time).

THE SUBJECT

Taxonomy

The Andean condor, along with six other species of New World vultures, belong to the family Cathartidae. The California condor most closely resembles the Andean condor both in size and color. The remaining species (the black, king, turkey, and the lesser and greater yellow-headed vultures) are all much smaller. Currently, the family *Catartidae* is placed in the same order, Falconiformes, as the Old World vultures of the family *Accipitridae*. Although vultures of these two families and hemispheres are strikingly similar in appearance and general behavior, they may represent examples of extreme convergence. According to Ligon (1967) , evidence from osteological characters, myology, and plumage, as well as some behavior patterns, indicate that the New World vultures have tighter evolutionary affinities with storks, the Ciconiiformes, and belong instead to that order, whereas Old World vultures should retain their ordinal position with the birds of prey. This study makes some comparative references to storks, because of this possible evolutionary tie, and to a number of studies of some Old World vultures because of the similarity in their niche or role as avian scavengers. Among The New World vultures, most comparisons are made with the California condor not only because of the close evolutionary

affinity but also because of the compendium of behavior and ecology data available from the studies by Carl Koford (1953) .

Description

Andean condors weigh about eight to 12 kg, and wingspans range from about 260 to 315 cm. Plumage of the immature bird is brown; the adult is black and white. Adults have a white collar and white patches on the dorsal surface of the wing. Sexes are dimorphic. Males are larger; they bear caruncles or crests on their heads, and the iris of their eyes is light brown (Plate 5). Females lack crests (Plate 6). The irides of immature females are light brown, those of adults red. The California condor is about the same size as the Andean condor, but the sexes are not dimorphic. Adult *Gymnogyps* are also black and white, but the white wing patches are on the undersides of the wing. With *Vultur*, both secondary and covert wing feathers are marked with white, whereas only the under wing coverts are white on *Gymnogyps*.

Age-Related Characters

Crests are present on the heads of newly-hatched male chicks. These crests grow more than the head during maturation, developing from a small bump to a large, fleshy protuberance almost as large as the rest of the head. The crest of a captive immature male about six months of age was 63 mm long and 20 mm high; nine months later, these dimensions were 70 mm and 25.5 mm. Dathe (1952) recorded a crest length of 8 cm for a bird 5-years-old; at 7 years, it was 9 cm and 4 cm high, and the dimensions were 10 cm and 4.5 cm four months later. The crest lengths of 30 dried adult heads measured on Isla Santa Rosa, Peru, ranged from 76 mm to 125 mm, with a median of 100 mm.

Male crests were individually marked and shaped. In Colombia, we recognized specific

Plate 5. An adult male condor.

Plate 6. An adult female condor.

adult males on the basis of crest differences. Many tilted to either one side or the other in the front or the back; some of the larger wart-like projections were distinctive. The size of the skin flaps hanging from the chin could not be used to age females. We saw females with immature plumage bearing larger flaps of skin than those of some adult birds.

Beak coloration might be a good indicator for two stages of immaturity. The beak of a captured immature male was all black when he was about six months of age; at the age of 12 months, however, gray patches appeared on the sides of the upper mandible. Then, less than a year later, the patches became whiter, while the ventral, distal part of the lower mandible also turned white.

Using plumage characteristics, I recognized four distinct age classes for wild condors: three levels of immaturity (stages 1-3) and the adult (Table 1). Plumage changes during maturation are described in the following section.

Molt

The captive immature male first began dropping feathers at the age of 1.5 years, about a year after he was taken from the nest. The innermost primary feathers of the wing dropped first, with the sequence moving distally. When about half of the primary feathers had dropped, tertiary feathers began to fall, apparently with the innermost dropping first. Then secondary feathers molted. In general, the outermost secondary feathers dropped first but not in the simple pattern of the primary feathers. Some secondary feathers did not drop until other more proximal feathers had fallen and were half-grown. Molt patterns of the two wings were nearly synchronized until secondary feathers fell; then the pattern of replacement began to differ between wings. Dathe (1952) also noted that patterns of secondary feather replacement differed between wings.

Table 1. Plumage characteristics used in identifying age class for either sex of condor.

	Plumage Characteristics	Estimated Age (years)[a]
Immature stage 1	Brown body and wings grey collar	0.5 - 4
Immature stage 2	Brown body and wings, white collar	4 - 5.5
Immature stage 3 (subadult)	Black-brown body, white-grey wing patches, white collar	5.5 - 8
Adult	Black body, white wing patches, white collar	>8

[a] Age estimates are based on data from captive animals studied by Onelli (1910), Dathe (1952), Lint (1959), R. Faust (pers. comm.), and the author.

Flight feathers often did not fall until the new feathers adjacent were about a quarter to half grown. The first full molt of remiges lasted about 18 months, but major changes in the captive bird's environment may have prolonged the molt unnaturally. In Paracas, Peru, the first flight feathers dropped in December 1969; none fell for the next three months, however, after the bird had been sent to Montana. A number of remiges began dropping again in August 1970 and then ceased when the condor was taken to Wisconsin in September. The molt did not continue again until November; it then progressed without interruption until June 1971; all juvenile flight feathers were replaced. According to Todd (1970), the full primary molt of a captive *Gymnogyps* took two years.

The rectrices of the captive *Vultur* molted simultaneously with the remiges. Central tail feathers dropped first, and replacement proceeded laterally. New coverts and body contour feathers appeared at the same time. Subsequent molts began in January 1972 and May 1973, but I did not record any information on the patterns or completeness of the molts.

The collar of the 4-year-old captive began to turn lighter in color, becoming light whitish-gray at the age of about 5.5 years. New secondary wing feathers grown when the bird was 5-years-old were lightly bordered with gray markings in areas that are white on adults. New wing coverts also showed less brown and more gray. These changes in color agree with those observed for other captive birds of similar ages (Table 1).

Observations on immature, sub-adult (stage-3 immature condors) and adult females feeding together at baits near Paracas, Peru, indicate that the white and black wing patterns are completed with two molts following the stage described above for the captive immature male (between 2 and 3). One female (#4) had markings like the 5.5-year-old captive male. The wing patches of another female (#3), almost complete on the dorsal surface of the wing, were gray; several of the innermost secondary feathers were only bordered with gray like those of female #4

and apparently were soon to be replaced. On another female (#2), the adult plumage was complete except for several of the innermost secondary feathers, which were gray like most of those of female #3. If the adult plumage of wild birds is attained at the age of 8 years, as it is with most captive birds, secondary wing feathers and coverts must change annually during at least the last three years before adult plumage appears.

The eyes of the adult female (#1) were red, and her collar was the thickest of the four females, whereas the eyes of female #4 were brown and her collar was the narrowest; the two features were represented in transitional stages among the four according to the presumed age rank.

The pattern of replacement for wing coverts was apparent on a number of wild birds due to color changes in succeeding plumages. In general, replacement of the greater secondary coverts preceded that of the median secondary coverts; the latter were replaced before the lesser secondary coverts. In each row, the outermost or distal coverts dropped first.

Head and Neck Color

Skin color of the head and neck seems to be related to the age of the bird, the area where they live, and to temporary internal conditions. In general, younger birds had darker heads and necks, whereas the skin color of the adults was lighter and more pink or red in color. The skin color of the four females above differed in this way: The head and neck of the bird assumed to be the youngest was grayish black, while that of the bird deemed oldest was pink. The color of the other two was intermediate. Usually, any pink or red coloration apparent on younger birds was restricted to the lower neck area just above the collar. The neck and head of younger immature condors seemed to have more down feathers.

Neck and head colors of birds observed in the Paracas study area appeared markedly

darker than those of Colombian condors. In the warmer climate of Colombia, condors appeared to avoid the midday sun, whereas condors may have sought exposure to the sun throughout the day on the cool Peruvian coast. This difference in sun exposure might explain the difference in pigmentation, although racial differences are possible.

We often noticed that head and neck coloration changed on individual condors visiting our baits. The head and neck skin frequently appeared to flush as condors fed and interacted. The head and neck of departing birds often seemed more pink or red than when they arrived. Sometimes, during aggressive encounters, the skin covering inflated crop areas appeared more yellow than usual. Todd (1974) noted that head color of a captive *Gymnogyps* became more intense when the bird was excited.

CHAPTER 2. THE CONDOR IN ANDEAN CULTURE

The condor has often played a dramatic role in the cosmology of Andean peoples. In some instances, the bird's role described the culture's history and destiny. Long before the rise of the Inca civilization, some South American people painted and wove beautiful representations of the bird and buried them with their dead. The Incas believed the condor had a role in creating parts of the Andean world and helped maintain the daily rhythm of earth and sun. After the Spanish conquered the Incas, both victor and conquered may have viewed the condor as a symbol for the fate of Andean natives. Today, some fiestas in more remote areas of the Andes act out charades of revenge, where condors are captured to do battle with a symbol of the Spanish conquerors. In northern Peru, another present-day fiesta, where condors are killed, may once have represented Spanish efforts to destroy the pagan culture of the Incas.

Whereas most city-dwellers in the Andean republics today have never seen a condor, many country people of the sierra, or serranos, are familiar with the bird and believe it has magical powers that can help them in their everyday lives. Like the eagle in North America, the condor represents strength and courage, but in a manner more profound and explicit, especially in Peru and Bolivia.

The word "condor" originates from the Spanish pronunciation and spelling of the quechua word *cuntur*, the native name for the big vulture. Quechua or runasimi was the language of the Inca nation. The first known written description of the word for condor came in 1560 in the Lexicon by Fray Domingo de Santo Tomas as "*condor-quebrantahuesos ave*" or "condor-bone-breaker bird," an association perhaps with the lammergeyer of the Old World, which is often called "bone-breaker." The name, Cerro Cunture, with the quechua spelling and pronunciation for condor, applies to a number of different mountain peaks in South America; one

of these mountains stood at the edge of our Colombia study area.

LEGENDS AND LORE

One of the native legends from the Department of Ancash in Peru tells of a fox that longed to have the bright and clean markings of the condor (Yauri, 1961). He pleaded at length with the condor to divulge the secret of his whiteness. The condor finally relented and agreed to help the fox change the color of this coat. At midnight he took the fox to the snow fields of the Cordillera Blanca and dropped him there. When the condor returned several hours later, the poor fox was dead. The story illustrates a typical position of the condor in Peruvian lore, a bird with awesome character able to withstand the elements of any altitude, a being worthy of respect.

As a figure of antiquity, the condor was present at the inception of the world and the Andean sphere. The sun served as the centerpiece of Inca cosmology and culture, and only the condor had the royal charge of tending to it. Every day the condor was to carry the sun out of the sacred lake of Wynaqocha to its zenith in the sky, release it, and let it fall back to earth (Barrionuevo, 1969). The condor was present at the sounding of the old city of Quito (Baudin, 1961). Quitimbe, its founder, went there after fleeing from giants. His wife, bitter at being abandoned, prepared to kill their son, but a condor came and took the child to the mountains.

Near Sicuani, Peru, we were told how a condor made the first hummingbirds. A condor, appearing as a handsome young man, lured a maiden from one of the village near Sicuani. He changed back into a condor and hid her in the mountains, where she bore him a child. Both mother and child were rescued, when a parrot revealed their location to the townspeople, the angry condor caught the parrot and swallowed him. When the parrot appeared once more, the enraged condor tore him apart and swallowed each piece. This time, the first hummingbirds

appeared.

Today, many highland Indians still believe that the condor can impart magical powers to them, especially in sickness. Parts of the bird are used as potions or medicines (Plate 7). Feliciano Mendozo of Nazca told me that, in the area of Puquio and Nazca, condor skins and feathers are used for many ailments and problems. Feathers placed under the beds of children ward off nightmares and help prevent bed-wetting. A *piska* (Plate 8), a bag made from the head of a condor, is used to wipe perspiration from the face to help cure colds and *sorroche*, or altitude sickness. If a maiden plucks feathers from a *piska*, it is believed they will grow back if she fills it with wine. Generally, *piskas* are used for carrying coca leaves, the commonly used Andean narcotic. Enchanted *quenas* or flutes are made from the right ulna of a condor. Eating pulverized condor heart aids cardiac problems, stomach mucosa heals breast cancer, and roasted eyes of condors make one's vision sharper (Apolinar, 1914 ; Housse, 1940). Broth made from a young condor controls madness (Baudin, 1961). The tongue can be taken for epilepsy. Drinking the blood of a condor will lengthen a person's life. Condors extend their own lives eternally by bathing in the waters of Lake Waynaqocha (Barrionuevo, 1969).

Behavior of the condor has been used both in the past and present to foretell future events. The flight of the condor after the condor-bull fiesta bodes well for the village. It is said that, before the conquest, the Inca priests of the sun foretold the fall of the Inca empire after seeing the flight of a wounded condor (*op. cit*). In Cotabambas, Peru, villagers told us that they expected a good corn crop because of incantations performed by the ***brujo*** or witch-doctor during the time of seeding; parts of the condor were used in the rites. For each of the *aukis* or spirits of twelve sacred peaks, the *brujo* burned an offering in a cave at midnight. Each offering, or *alcanza*, contained three coca leaves, three coca seeds, a piece of pure suet from the llama, scrapings from the claw of a puma and the beak of a condor and a sea shell, a special paper of

Plate 7. An adult male condor skin for sale in the Ica market.

Table 8. A *piska*. A bag for coca leaves made from the skin taken from the head of an adult male condor.

gold and silver called *ccorilibro*, and corn of three colors; yellow, white, and red. All of this, the *brujo* wrapped in a clean corn sheath and burned it in a sacred place. Smoke from the burning *alcanza* traveled to the mountain and to the *auki* or spirit for which it was destined.

CONDOR-BULL FIESTA

In some of the more isolated mountain villages of southern Peru, condor-bull fiestas, or *corridas de toros con condores*, are practiced annually. These elaborate and extended celebrations seem to have originated as symbols of Indian triumph over the Spanish conquerors. The legs of a live condor are tied to leather strips threaded through holes pierced in the hide on the sides of a bull (Plate 9). The bull is released and baited by men waving their ponchos. The condor bites at the bull's ears, back, or sides where his legs are tied. The bull leaps and turns and throws his head and horns back toward the condor he carries. Usually within one-half hour, the bull tires and is tied down with many ropes so the condor can be removed. After a few days of rest, the condor is taken to a certain ridge or mountain to be released. In the release, as in the week of activities preceding, long processions file through the village. Colorful lines of brightly dressed people dance and sing. At the head of the procession, two men carry each condor, swinging the bird by the wingtips with each stop (Plate 10). When the condor is set free, they continue to sing and dance until the bird flies. As the condor, the Indian is native to the Andes; in the celebration of revenge, the condor is a victorious symbol of the Indian and his dying culture. The bull came from the Old World and represents the conqueror and the wealth of the ruling elite. If the condor can fly after meeting the bull, the vindication is successful and represents a good omen for the village. In some fiestas of the past, as the last gesture of revenge,

Plate 9. A condor-bull fiesta in Cuzco in 1969.

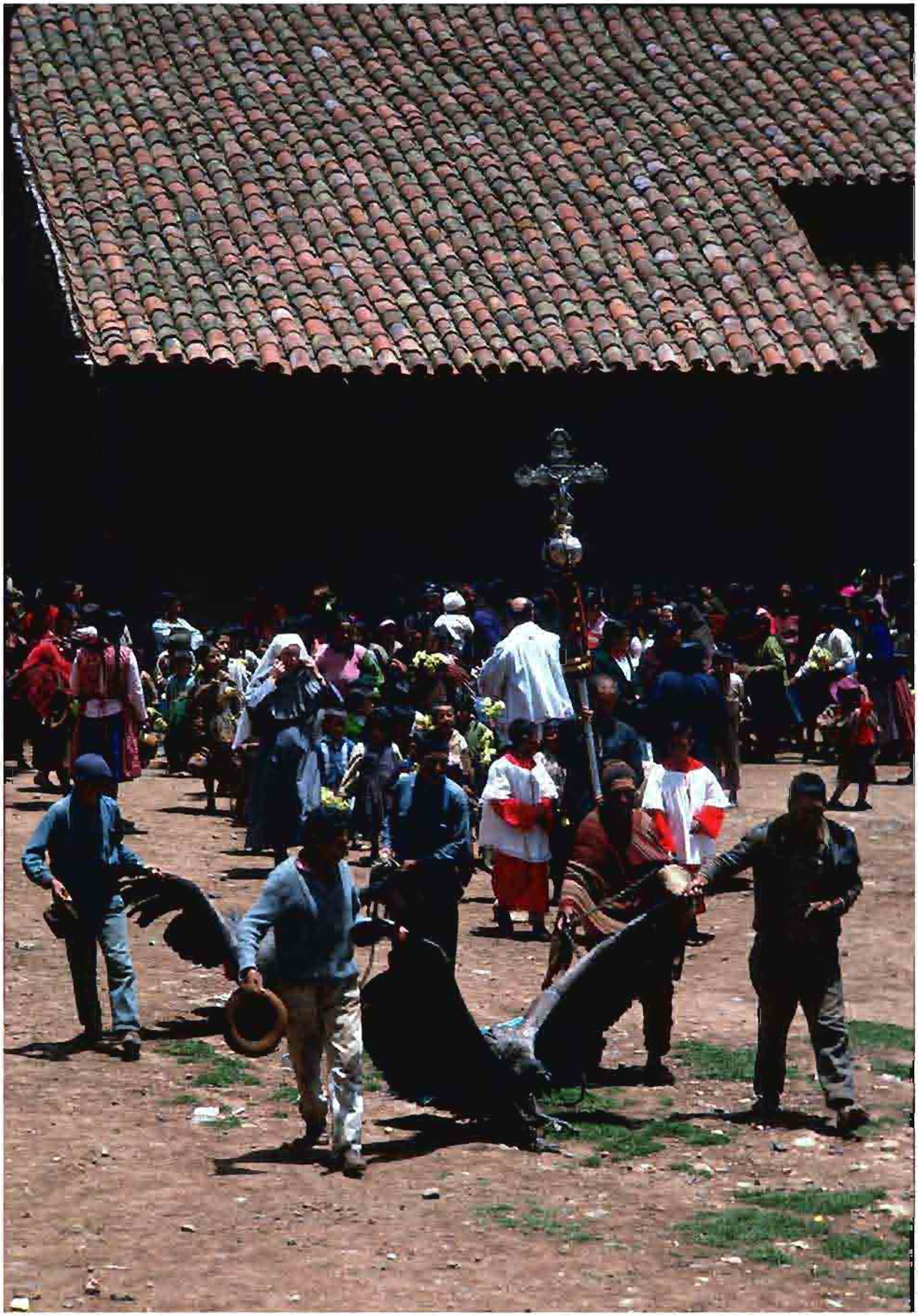


Plate 10. A procession to the condor-bull fiesta in Cotabambas, Peru. 1969.

the bull was put to death after the condor had ridden him.

Although modern accounts of the condor-bull fiesta frequently describe the symbolism of the struggle (Sabogal, 1949 ; Rouvre, 1957 ; Barrionuevo, 1969), only a few of the people that watched and participated in the fiestas we saw knew of the representations. The earliest record I could find was an account from the 1870's with both a description and photograph of a condor-bull fiesta (Squier, 1877).

In the town of Cotabambas, the condors used in a fiesta we witnessed were treated as though they had supernatural powers. May of the villagers believed that the condor would return and destroy the livestock of any man that mistreated it. Anyone causing the death of the condor would also die. Before the condor was captured, a *brujo* had done incantations over the bait horse at midnight. He was responsible for the lives of the birds after they had been captured. During part of the fiesta, when it appeared that one bird was injured while being tied to the bull, the *brujo* had to be physically restrained by a group of men that watched over him. He tried to get to the condor, but they did not permit it.

The week-long celebration that culminates in the condor-bull fiesta is sponsored annually by two townspeople selected each year to compete in providing the best food and entertainment. They give feasts, bring in bands, fireworks displays, and amateur bull-fighters from Cuzco, pay for the capture of the condor, and arrange for the bulls to be used. Several villagers told me that in the past, if one *dueño del cargo* or sponsor appeared to be losing the competition, he enlisted the help of the *brujo* to put a hex on the festivities of the other *dueño*. To do this, the *brujo* sat on a special corner of the town square and scraped the claws of a dead condor.

In the *despedida* or farewell, the condor is often marked before the release. Torres Blanco of Cuzco told me that in Paruro, two days after the struggle, the condor was released with a ribbon tied through the crest and a necklace with three small bottles. One bottle contained

chicha or corn beer, one wine, and the other *aquardiente*, a kind of anise brandy. It is believed that after the condor flies he finds and serves the other condors with the drink that he bears, and then they respect him as the villagers respect the *dueño del cargo* or *capitan de tores*, as he is called in Paruro. Torres Blanco told me he once saw a marked condor three days after the *despedida*; the bird still carried the ribbon on his crest but the necklace was gone.

The condor-bull fiesta appeared to be declining during the period of our study, except in larger cities like Cuzco where it was revived on one occasion as a tourist attraction. When we were in Peru the only small villages still holding the fiesta were in isolated areas. As villages begin to fall under the influence of nearby cities, the rewards of being a *dueño del cargo* probably diminish relative to those offered by the modern world. The expense involved the *dueño* or *capitan* is so great that, in the past, some have sold their homes for this honor. Sacrifices such as these would probably continue only in those areas relatively isolated from the goods and distractions of a modern world. Condors apparently are becoming more difficult to find; some villages reportedly have resorted to the use of hawks in the fiesta. Feliciano Mendoza told me that in the last decade condors have disappeared from many areas between Puquio and Nazca, where they were once common.

In November 1970, the condor-bull fiesta was outlawed in Peru. Because most fiestas were practiced in isolated areas only, they may well continue in small numbers beyond the eye of whatever small enforcement staff exists to counter them.

THE CONDOR RACHI

During *carnavales* celebrations in some isolated villages of the Callejon de Huaylas region of northern Peru, condors are suspended from rope arches and beaten to death by

horsemen that ride below. One end of a rope suspended between two poles extends on down to the ground. By pulling or releasing this end, one man controls the height of the hanging bird. The riders, around 10 to 15 men, ride beneath the moving arch and attempt to strike the condor with their fists (Plate 11). The ritual beating usually lasts about one hour. The bloody ritual ends when the condor is ripped apart and completely dismembered (Plate 12).

At the beginning of the celebration fruits and bottles of *chica* are tied to the rope for the horsemen to take. When the last prize is gone, they suspend the condor and kill it. Then the tongue is bitten out of the condor by the man who will be in charge of capturing a condor the following year. The dead bird is lowered to the crowd and torn apart. *Rachi*, a quechua word, means "the-tearing-apart-of."

Even though we observed two of the fiestas, I obtained little material on the condor in the folklore of that region. Sources available in the National Library of Peru provided no information on myths or symbols involving the *rachi*, although one book described the fiesta in detail (Huascaron, 1952). We met a missionary at one fiesta , however, who gave the following account for the fiesta's origin:

> In the *corta-monte*, another fiesta of that region, a tree filled with presents is slowly cut down while villagers dance around it. In this, an Old World celebration, the tree once represented a pagan god of the barbarians. In one other celebration from the Old World, horsemen vied in a contest of skill to see who could pull the head off a live chicken suspended from a rope arch. From the elements of these two celebrations, together with the heathen identity of Indian and condor, came the *rachi*, a symbolic destruction of the Inca's pagan culture.

REPRESENTATIONS IN ART

The white collar and wing patches, the naked head and full crop, the perforated nostrils, and the male crest are all characteristics useful in recognizing the condor in ceramics, pottery

Plate 11. The *rachi* in Callejon de Hualylas in 1970.

Plate 12. A girl with a flight feather from a condor dismembered in a *rachi* ceremony. Callejon de Huaylas in 1970.

figurines, and etchings on the desert. The most accurate representations of condors we saw on relics were those of the Nazca culture, a coastal culture of southern Peru from about 0 to 900 A.D. In some weavings and polychrome ceramics, condors are easily recognized (Plates 13, 14, 15). The detail can be startling; neck flaps, full crops, and wrinkled skin on the heads mark some of the beautiful, rather abstract representations. Near the town of Nazca, where lines and animal figures have been etched on the gypsum desert by a people of unknown antiquity, there is one figure of condor-like bird bearing a large distended crop. As with most of the animal etchings, the figure is quite stylized (see Reiche, 1968 for illustrations of this and other remarkable desert drawings). A ceremonial fan made from the tail and wings of a condor was taken from a grave near Paracas and aged at about 2000 yr. old. Although the condor probably figured in the art works of numerous Andean cultures, we made no survey of that representation. Few motifs of the condor exist in contemporary works of art.

Plate 13. A polychrome bowl from the Nazca culture.

Plate 14. A polychrome stirrup-pot from the Nazca culture.

Plate 15. A weaving from the Paracas culture.

CHAPTER 3. GENERAL ACTIVITY

INTRODUCTION

This chapter deals with body postures, maintenance behavior, and weather-related effects. First, various postures and motor patterns are described in detail. Then, the settings in which the various patterns occurred are examined to evaluate what a particular pattern or posture does for the bird. What is the function of preening? Why do condors stretch? Do condors sun to warm themselves? The most commonly seen behavior patterns, often called maintenance behavior or comfort patterns, are familiar to every student of animal behavior, yet the precise reason for the pattern, its function, remains an enigma in many cases.

For the field biologist trying to discern the meaning of a behavior as elaborate as bathing or as simple as a head shake, the clues are found in the setting or context of the pattern. Do condors assume the sunning posture without exposure to the sun? Condors often defecate on their legs. Is this for cooling or perhaps for repelling parasites? When, then, and under what circumstances do condors defecate on their legs? If sunning served to warm the bird and defecation on the legs were for cooling, one would not expect both to occur at the same time.

In some instances, clues to the function of a behavior can be found by noting which other motor patterns tend to precede or follow it, that is, its context in pattern sequences. For instance, the idea that body shaking serves to rearrange displaced feathers gains credence when we find that this pattern tends to follow feather preening, an activity that shifts feathers from their normal position(Delius, 1969). Preening occurs frequently among groups of condors. Does it serve more than a maintenance function? Is it a communication signal of some type? One way to approach these questions is to analyze the frequency of preening patterns by condors alone and in groups. Is it seen more often in social situations? If preening serves to arrange barbs in the

vane of a feather, we might expect to find that preening patterns follow activities that disturb barb arrangement.

For three reasons, condors are superb subjects for such questions. First, the motor patterns of the condor are relatively deliberate, so they are easier to separate into distinct elements than those of most other birds. Second, condors were often visible on cliffside perches or roosts for hours at a time, so I could record lengthy sequences of different motor patterns and posture changes. Assembling these data in a chi-square matrix permitted me to identify associations of both positive and negative forms between patterns.[5] Third, recording these data for all periods of the day allowed me to examine the relationship between pattern frequency and the time of day. The temporal context of a pattern might clarify purpose. Do condors sun more often at certain times of day or at certain temperatures? Is stretching related to activity? Do we find the pattern occurring more often in the morning before foraging activity begins, or does it occur consistently throughout the day? Does preening occur more often at the end of foraging or before the onset?

Also in this chapter, I consider the relation between some behavior patterns and the weather. Sunning is clearly related to weather, but its function is not an obvious one. I examine perch selection with reference to sun and shade exposure of the site at the time of its use. Another section deals with how the onset of foraging relates to air movement. Another considers how the bird controls its internal temperature. Part of this last section examines the importance of factors like activity, ambient temperature, time of day, and light in thermoregulation. In summary, this chapter looks at the simple behavior patterns and postures of the Andean condor, catalogs their various contexts, and speculates upon their purpose. Three contexts considered in some detail here are (1) weather conditions, (2) time of day, and (3) the sequential position among other motor patterns.

COMMON PATTERNS

Standing, Sitting, and Lying

Condors spend about one-fourth to one-half of the daylight hours standing quietly. I watched one adult male stand motionless, except for infrequent head shakes for 97 minutes. The tarsi of a condor in the standing posture are nearly vertical; when the bird stands on a steep incline, the angle between the tarsi and the digits varies in a way that allows the tarsi to remain almost vertical. The short hallux provides no support. Digits No. 2, 3, and 4 lie flat on the perch surface. If the bird stands on a edge, these digits may extend over the edge and down along the vertical surface, but they do not actually grip.

Condors often sit on the tarsi. They may do so while bathing, while feeding on the lower part of a carcass, or while wiping the head and neck on the ground. During mating, the mounted condor sometimes sits. I frequently saw inactive condors at roosts and at nests sitting on the tarsi during various times of day.

A sleeping condors usually lies with its breast on the ground (Plate 16). Before lying down the condor sits. Frequently, the tail is elevated about 30^{o} above the long axis of the body and drops slowly just after the bird lowered onto its breast. In sleep, the head is usually turned toward the posterior and either rests on the back with closed eyes or is concealed, except for the occiput, below the scapular feathers. I watched the head of one dozing condor slide slowly from the back down across the wing until it hung inverted near the front of the wing. After 2-3 minutes, the head moved to the back again. This sequence of movements was repeated three times in 20 minutes. One male maintained sitting and lying postures for 170 minutes without standing. In saw condors in lying posture at all times of day.

Plate 16. An adult condor asleep on a ledge above the sea.

Walking

When a walking condor extends a foot forward, the posterior part of the body usually descends until the foot is placed and weight transferred to it. The body rapidly returns toward a more horizontal position. Thus, the long axis of the body may move through an arc in the sagittal plane that ranges from 30^{o} to 60^{o} with the horizontal during the gait. In fast walking, this rocking motion is reduced and may not change at all in running. During weight shift, the head often thrusts forward quickly. As the condor moves ahead while extending the other leg, the neck arches so that the body, advancing faster than the head, moves beneath the head. A walking bird usually directs the head forward and down at an angle 5^{o} to 10^{o} below the horizontal so if the collar ruff is raised to the chin, the bird intermittently fits the lower beak into the edge of the ruff and moves it out as the neck alternately arches and extends. The rocking movement of the body is absorbed by the neck so that the head moves smoothly and evenly parallel to the ground. When the foot is lifted from the ground, digits No. 2 and 4 are depressed down about two to three cm below digit No. 3 and compressed inward, laterally toward digit No. 3 about the same distance. Just before the foot touches the ground again, these two outer digits resume the extended position. The wingtips and tail sway laterally toward the side of the advancing leg and the body tilts slightly to that side. I saw two immature condors walking side-by-side bump wings each time they extended the inside foot simultaneously.

For condors approaching a food source, the rate of walking in seven observations ranged from one to four steps per second, with an average of two per second, the usual rate. Koford (1953, p. 29) reported a normal unhurried speed for the California condor of about one step per second. According to Fisher (1946), the Andean condor is better suited anatomically for walking and running than the California condor. An Andean condor visiting several dried

pelican skins on a level beach walked 0.5 km when wind conditions would have permitted flight.

On the Peruvian coast, condor tracks in the sand provided additional information on the gait (Figure 5). In eight measurements from five different track sets (likely made by different birds), the distance from one track to the next varied from 40 to 66 cm, with a median of 48 cm. Although the tracks were found on inclines with angles varying from 0^o to 35^o, I found no discernible difference in the track patterns or interval distances related to slope. The location of each heel print varied from 0 to 5 cm in distance lateral to the projected center line of travel.

Sometimes condors walk backwards. On three different occasions, I saw condors land upwind from a feeding site and walk backwards to the food as they maintained the anterior part of the body directed in to the cold 30 to 40 km/hr wind. In each case, the bird glanced over its back as it walked. This peculiar orientation probably served to avoid feather displacement by the wind. An adult female missing one foot and tarsus moved about on the ground by hopping. Unlike other condors, she moved sideways as frequently as she did forward.

Running, Bounding, and Climbing

In running, condors frequently lower the neck and extend and flap the wings. When taking off, the running gait changes to a series of bounds; in each bound, the lead foot strikes the ground a moment after the other. Each hop carries the bird across distances up to 2.5 m. Tracks in the sand indicated that condors taking off usually bound progressively farther with each successive stride until airborne. An exception, where interval distances between each pair of tracks remained constant, went up a 5^o to 10^o slope. For one track series on flat land, the distance between the print pairs increased progressively from 66 cm to 129 cm across seven hops before the condor was airborne. The short distance between the prints of each pair increased from 19 cm to 47 cm. One leg may exert a greater thrusting force; if so, condors might have and

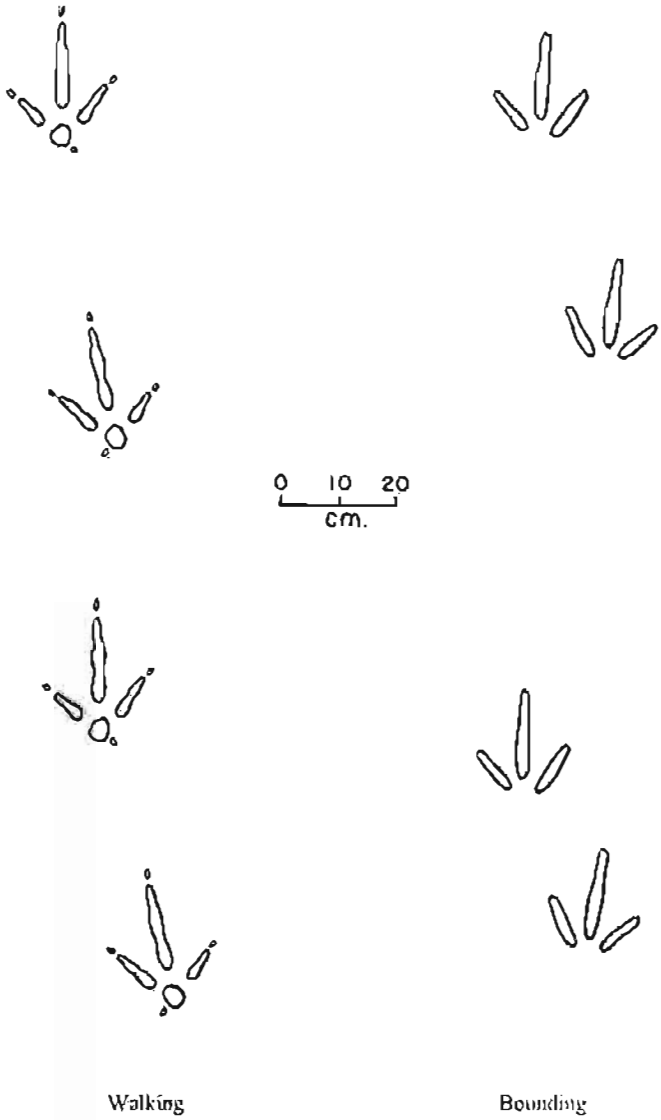


Figure 5. Condor tracks in the sand on the Peruvian coast.

favor a stronger leg as the lead or back foot in the bound. The leg leading in each pair of prints remained constant within the set in 25 different sets of tracks by birds taking off. In 19 sets, the leading leg was left, in six the right.

The tracks of walking condors demonstrated a foot orientation with digits No. 3 either parallel or turned inward up to 10^{o} with the projected line of travel. The tracks of bounding condors, however, showed digit No. 3 directed up to 10^{o} away from the line of travel (Plate 16). In track pairs make by bounding condors, the leading foot tended to turn out less that the other. Typically, the distal parts of each digit were imprinted more deeply in the sand. A bounding condor usually left no heel print.

Condors frequently climb slopes before taking off. Three condors climbing 200 m up a sand and rock slope with a 60^{o} angle of incline maintained a more erect body posture and more extended legs than was typical of movement on level ground. Condors climbing down steep inclines usually crouch near the surface, extend and lower their neck and head, and flap partially extended wings over the back as they move about. The brachia, forearms, and occasionally the manus are extended vertically. The angle between the crus and the tarsus may decrease to 30^{o}. Condors often side-step down hill. Wing movement and crouching apparently serve in maintaining balance.

Preening

Motions associated with feather manipulation by the beak are of two general types. The mandibles grasp large feathers of the wing or tail singly and move from quill base to or near the tip. During the preening motion, the feather is pulled from its usual position but snaps back after slipping free. Nibbling motions, used with smaller feathers, often move across an area of many feathers before the condor looks up or moves its bill to preen another area on the body. In

preening the base of the neck, the condor frequently moves from the breast around to the back and returns without ceasing the nibbling motions.

By recording the frequency or preening occurrences according to the body region preened, I found that the neck, breast, and wings accounted for over half the occurrences tallied, whereas the rectrices and oil gland represented only three percent (Table 2). Many of the condors observed preening in the tail covert region presumably nibbled at the oil gland.

Often the tail was lifted and partially spread as the condor preened in the coverts near its base. A wing usually drooped when the condor preened beneath it. Sometimes the wing relaxed at the elbow enough that the primary feathers touched the ground. The wing was reset after the condor moved to preen elsewhere although occasionally I saw a condor preening on the back or breast while a wing still drooped or the tail, recently preened, remained elevated and later descended slowly toward the normal position.

Preening is the most common activity of perched condors. Bouts range from several seconds to half an hour. One adult male observed in Colombia for 4.5 hours preened for a total of 65 minutes, 24 percent of the observation time and 67 percent of the time perched (Table 4). Sometimes bouts of preening ar broken by long periods of inactivity. On different days I recorded three periods of 168, 110, and 59 minutes in which a perched male condor did not preen. Davis (1974) estimated turkey vultures that she observed spend roughly half of their roosting time in preening.

I saw three different condors preen during soaring flight. An adult female and an adult male preened feathers at the base of the neck and wing for about 15 seconds. Another adult male preened breast, neck, and wing covert feathers for a full minute while soaring. Koford (1953, p. 25) once saw a California condor preen at the base of the neck briefly while soaring. Andean condors in the sunning posture sometimes preened their wing coverts, breast, neck and back

Table 2. Percent preening occurrences tallied according to the body region preened. Recorded for wild adult condors on eight different occasions. These data do not reflect differences in preening durations at each site.

	Percent of occurrences recorded for region listed									
No. observations	Neck	Breast	Back	Left shoulder	Right shoulder	Left side	Right side	Left wing	Right wing	Rectrices & oil gland
281	16	16	11	6	6	5	10	8	18	3

feathers although preening activity usually ceased when the birds started sunning. Condors in the lying position seldom preened. Preening frequently occurred during or following encounters with other condors. Subordinate condors displaced from feeding sites often stood nearby and preened actively. One adult female immediately began preening after copulating. I observed condors preening other condors occasionally at roost, nest, and feeding sites. On a regular basis one male parent preened a nestling for extended periods. I never saw a condor preen the large flight feathers of another condor. Preening in most of these examples probably serves as more than the arrangement of feathers or feather parts and acts instead or additionally as a communication signal.

Bathing and Drinking

The motor patterns of bathing by wild and captive condors were similar and of four principal types. After extending the feathers out on the belly and abdomen, the bird lowers the body and thrusts its abdomen forward in the water, while the wings with flexed manus snap up just above the back. The body rocks back to the original posture. Movements are abrupt. Sometimes the bird sites in the water during this pattern (Figure 6a). In the second pattern, the neck is extended vertically, one folded wing is advanced forward so that the wrist extends 15-25 cm forward of the normal position, and the body leans toward that side dipping the wing into the water. The wrist and forepart of that wing remain next to the body, while partial extension of the brachium moves the elbow out 20-30 cm toward and usually into the water (Figure 6b). In the third pattern, the bird, either sitting or standing, dips forward and extends the head and neck below the surface of the water. Just before returning to the upright position, the neck flexes to snap the head posteriorly, throwing water on the back (Figure 6c). Simultaneously, both wings, with the forearms and manus flexed, flap simultaneously against the sides, moving out and above

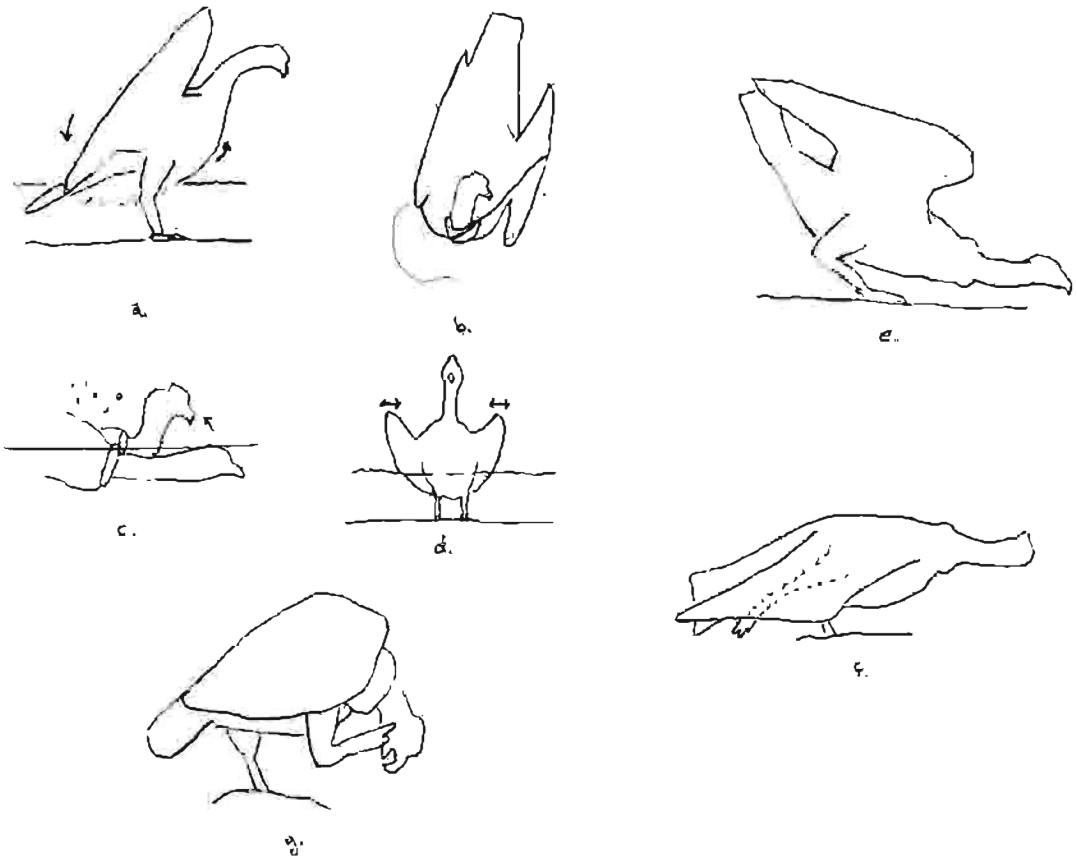


Figure 6. Some body maintenance behavior patterns: a-d four bathing patterns, e bow stretch, f side stretch, g head stretch

the back about 10-15 cm from the body (Figure 6d). Both captive and wild condors enter the water, bathe without pause using these motions in various sequences, and then step or leap out. Gailey and Bolwig (1973) reported that two captive adult Andean condors sometimes submerged completely and rolled over while bathing. Motor patterns of bathing by the California condor are similar to those described above (Koford, 1953, p. 75). An Andean condor that I held captive usually presented all four of the patterns when I splashed water on him. In Colombia this captive bird bathed every day (Figure 6).

The condor often drank while bathing, taking a beach full of water and swallowing it while holding the head in a normal level posture. The beak was not tipped upwards in the usual avian drinking movement; nibbling motions occurred throughout the pattern. I once saw an adult male drink before bathing. In other separate instances, I watched an adult male and an adult female fly to a pool, drink five times each, and then fly again. Usually they held the beak below the feet out of sight for just less than one second before resuming upright posture. I saw now other instances of drinking by wild condors.

Durations of Bathing.

Condors usually bathed in sequences of short bouts. In a 14-minute period, an adult male (AML) with a very full crop bathed five times for about 15 seconds each about. He stopped up out of the pool, preened, and sometimes shook during the interims. All of the body feathers appeared to be wet after the last bout. Then he preened and sunned near the pool. Once I saw AML and AFL bathe together for 15 seconds. In the preceding 10-minute period, the male had bathed for about 1 minute alone in another bout and the female alone for 23 seconds. After bathing together AML returned for another 28-second bath, and AFL returned twice for a 20-second and a 19-second bout. As they bobbed about during the bath, water was thrown up over their backs. Afterwards both wet birds preened and sunned.

Bathing and Drinking Sites.

On three different occasions, I saw AML and AFL bathe in a small pool of water on a central ledge in a palisade of cliffs. The same pair, on three other visits to this pool, drank but did not bath. The pool, situated 150m below the canyon rim in the center of the pair's roosting cliffs, was surrounded by grasses and bromliads. I was unable to determine the pool's dimensions. On the same series of cliffs 300 m farther downstream, I saw AF2 drink from a pool near her roost and nest. The pool occupied a grass ledge about 75 m below the top of the canyon. Park 2 probably used this pool for bathing also. California condors also prefer to use water near their roots (Koford 1953, p. 74).

In the Cerro Illescas, I found a bathing site at the head of an isolated canyon, Quebrado Nac. The pool, 2 m in diameter and 10 to 15 cm in depth, was fed by a saline spring. A large boulder 8 m above the pool was completely covered with bird excrement. A series of about 15 rocks, all covered with excrement, extended on up to the top of the ridge about 150 m above the pool. In and around the pool were condor tracks and feathers. The water contained algae and was less saline that ocean water. I never saw condors bathe in the ocean. Several Peruvian fishermen near Pisco reported that condors never used the ocean water but frequently bathed in a fresh water estuary on the coast southwest of Ica. I never saw a condor dust-bathe.

Stretching

As with most bird species, the Andean condor uses two patterns of stretching. The two types occur at about the same frequency. In contrast, among California condors, bow stretching, apparently occurs only about half as often as the other pattern, the side stretch (Koford 1953, p. 27). Motor patterns of both forms appear to be similar for the two condors.

The Bow Stretch.

Both wings are extended in the bow stretch. The manus remain flexed, but the upper arms and forearms are partially extended so that the wings are held above the back with the wrists 30-50 cm above and lateral to their normal position against the body. The body dips forward until the neck nearly touches the ground. The long axis of the body forms an angle approximately 45^{o} with the horizontal. The neck is bent slightly in the middle so that the distal portion is parallel to the ground. The tail is spread and elevated so that its long axis becomes nearly vertical. The wings remain partially extended during the dip up and down and during the pause in the bow stance. The complete pattern lasts 4-6 second (Figure 6e), approximately the same duration observed for turkey vultures (Davis, 1974).

Condors frequently bow-stretched immediately after completing a side stretch. Before the single extended wing was completely retracted, the other wing was extended partially and the bow stretch began. I saw one condor bow-stretch immediately after landing and before the wings were folded. Certain social settings may facilitate bow stretching. Four different times I noted one individual of an adult pair bow-stretch immediately after its mate had.

The Side Stretch.

The stretch movement begins when one wing is fully extended downward 30^{o} to 60^{o} below the horizontal flight position and toward the rear at an angle about 60^{o} from the long axis of the body. Then, as the body dips forward to a level position, the head and neck are lowered and twisted toward the side opposite the extended wing. Simultaneously the leg below this wing is fully extended in the same direction as the wing. Half of the tail on that side is fully spread. After a pause, the tail and leg are retracted to the usual position, and then the body resumes the normal stance as the wing is folded (Figure 6f). Eight durations measured for the wing extension in this pattern ranged from 6.5 to 9.5 seconds, with a median of 9. Davis (1974)

reported side-stretching by turkey vultures lasted 6 to 8 seconds.

Condors perched on inclines usually side-stretched away from the cliff or hill. In 18 observations of this behavior pattern, 16 were of stretches performed with the extended limbs directed away from the perch strata. One adult male side-stretched the right side three times in 22 minutes without ever stretching the left on the side facing the cliff. In one instance, a condor that did stretch toward the cliff was unable to completely extend the wing. I saw adults defecate during a side-stretch; each bird raised it tail slightly and defecated while the wing was extended and body dipped forward. After defecating, the leg and tail were extended, and the stretch continued normally. I observed both bow stretches and side stretches performed by nestling, immature, and adult condors at the roost, on day perches, at the nest, and at feeding sites.

Body Shaking

Before a condor shakes, the body feathers are erected. After a pause, the folded wings shake alternately at least twice, and the body moves briskly from side to side. The brachia extend partially so that the wrists move out laterally about 15 cm, and the wings are then shaken up and down through an arc up to 30 cm in length. By tipping the distal ends of the brachia up the wing tips are held above the rest of the wing and up to 1 m above the ground during the shake. Sometimes the wing, flexed at the manus, is extended vertically above the back after the shaking movements cease. The tail, neither compressed nor expanded fully, is shaken laterally in rhythm with the wing movement. The complete pattern typically lasts 2 to 3 seconds and is often followed by a quick head shake. Body shaking by the turkey vulture is of about the same duration (Davis, 1974).

When body feathers slowly extend out from the back and belly of a condor that is

preening actively, a body shake almost always follows. Preening ceases during the shake. Body shaking seemed to occur more frequently during periods of bathing activity. One adult male shook three times in a 16-minute period during and following a bath. The movements involved in shaking the body produce a rustling sound clearly audible at 100 to 200 m.

Defecating

Movements used in defecating vary between two general types. In one, the body of the condor tips forward until the head and neck almost touch the ground. The tail ascends above its normal position, and a body tremor precedes the forceful discharge of excrement. Sometimes the wings, folded at the wrist and elbow, are extended at the brachia 5 to 10 cm above the back during the motor pattern. I saw this pattern used regularly by condors that had not defecated for extended periods, some as long as three hours. Large quantities of excrement, often over 100 g in mass, were cast behind the bird 30 cm to 1 m from the feet.

In the second general type, the head, neck, wings, and tail remain fairly stationary while the abdomen is thrust forward 2 to 10 cm toward the tarsi. They belly feathers extend out before this movement and then retract once the normal stance is resumed. Sometimes the wings are extended at the brachia laterally about 5 cm as the abdomen rocks forward and are reset after the body returns to the normal posture. The excrement is cast forward and usually lands on the tarsi or feet of the condor although occasionally I saw it land between the feet, sometimes directly below the anus, and once 10 cm in front of the tarsi. Usually the abdomen thrusts forward and rotates slightly toward the right or left, whereupon the excrement is deposited on the tarsus of that side. Elimination in this manner occurred when a condor defecated small amounts frequently. At a feeding site one sub-adult female deposited a single large drop of the white matter on her tarsus three times in five minutes. Condors defecating after alighting usually

deposited it on their tarsi. Condors used both manners of defecating while they fed. Once I saw an adult female discharge a white spray of excrement while in soaring flight.

Head and Neck Wiping

Condors of all age and sex classes frequently wipe the head and neck across their own back or upon another surface (Plate 10). Grass, sand, gravel, round or jagged boulders, or even a food carcass are used for wiping. An unusual pattern in birds, wiping apparently does not occur with some other bare-headed species that feed on carrion; Kahl (pers. comm.:26) has never seen it in any of the bare-headed storks. Koford (1953, p. 26) reported wiping by the California condor, and I have seen it by the turkey vulture.

For condors, the motor patterns involved in wiping on the ground vary considerably. Condors wipe the neck and head while standing with the body tipped forward, or with legs flexed so the body is in a crouched position and nearly horizontal, or while actually sitting upon their tarsi. Sometimes a standing condor drops to sit on the tarsi during the wiping activity. They often walk or shuffle forward on the feet or tarsi while twisting and turning the neck and head on the ground. Birds that do not walk about during this activity extend the neck forward and then retract it again or sweep it back and forth laterally while rotating the head and neck so the sides are in contact with the ground. A condor sitting on the tarsi sometimes rocks back and forth to push and pull the neck across the ground by leaning the body forward and then back. The crus forms an angle with the ground that varies from 45^{o} to 90^{o}. Occasionally during the wiping motions the condor opens the beak 1 to 2 cm, sometimes nibbling at the ground. The dorsal surface of the neck and head is wiped by rotating the neck and turning it to the side simultaneously so that the inverted head lies lateral to the wing, pointing rearward. Condors

Plate 17. Immature male condor wiping the head and neck on the ground. Note the impressions left in the sand by the lateral sweeping motions of the head and neck.

wiping in the sand frequently close their eyes. Sometimes they used several wiping postures and on several different surface strata in a single series of patterns.

On the Peruvian coast, with three general types of wiping strata available in roughly equal proportions, I observed condors using wet and dry gravel in 25 instances, sand in 23, and large rocks in 13. Bouts of constant wiping varied from 8 seconds to 1 minute in length. Sequences of wiping interspersed with short pauses often extended over 3- to 5-minute periods, although occasionally they lasted for 10 minutes.

Wiping the head and neck on the ground seems to clean food particles and gore from the skin. Condors were observed in this activity directly after feeding 77 times. I recorded 23 instances of ground wiping by nesting parents after feeding the chick. In only three instances did I note this pattern when I had not seen feeding activity precede it. In each case, however, it was possible that the condor had fed in another area within the preceding hour.

Wiping the head and neck on the back involves similar motor patterns but probably serves a different function. This activity was not seen in feeding situations but was regularly recorded during periods of preening. Generally the side and top of the head are swept back and forth three or four times across a 20-cm distance on the body feathers of the back. While wiping, the condor sometimes rotates the head so the chin is exposed dorsally.

Scratching the Head

The condor scratches its head with the foot by dipping forward, lowering and directing the head toward the feet, and scratching the cheek area with claw and inside of the distal part of digit No. 3 (Figure 6g). This pattern of "direct" scratching differs from that of most passerine and some non-passerine birds, in which the leg passes over the wing. In 24 observations, all contact was restricted to the head, usually to the cheek. The beak was touched occasionally.

Sometimes the beak opened during this pattern. In 14 observations, the numbers of scratching motions in each bout ranged from 3 to 22, with a median of 9. I found no apparent differences relative to sex or to particular side. Condors scratching on narrow ledges or steep slopes showed no tendency to use either the foot facing away or toward the perch stratum. Half of 12 instances were directed away, the other toward the incline.

I saw adult male condors scratch the head with the foot during soaring flight on three separate occasions (Figure 7). During the scratching bout of one soaring bird, the head appeared to rotate from side to side while the foot made eight contact motions. The wing angle of attack increased during the first half of the bout, and the bird appeared to ascend and decelerate slightly. The flight path leveled during the last part. Another male that made 10 to 15 scratching movements wile soaring appeared to maintain the same forward velocity. I saw black vultures scratch the head during flight in a similar manner, except that the head was not lowered quite as far. Koford (1953, p. 25) reported that California condors and turkey vultures also scratch the head during flight.

Shaking and Turning the Head

Head-shaking movements ranged from short single flips of the head to bouts where head and neck swung from side to side or up and down. The larger movements appeared related to disgorging. Sometimes a condor pointed the head toward the feet and shook it laterally just in front of the breast with little or no neck movement. The most frequent type of head shaking was a short head flip by a bird in a normal erect stance. The head rotated to one side about 60^{o}, flipped to the other side, and then turned forward again in one quick smooth sequence. Occasionally, a simple head shake by the captive immature condor was accompanied by a sneezing sound and a discharge of watery spray from the nostrils.

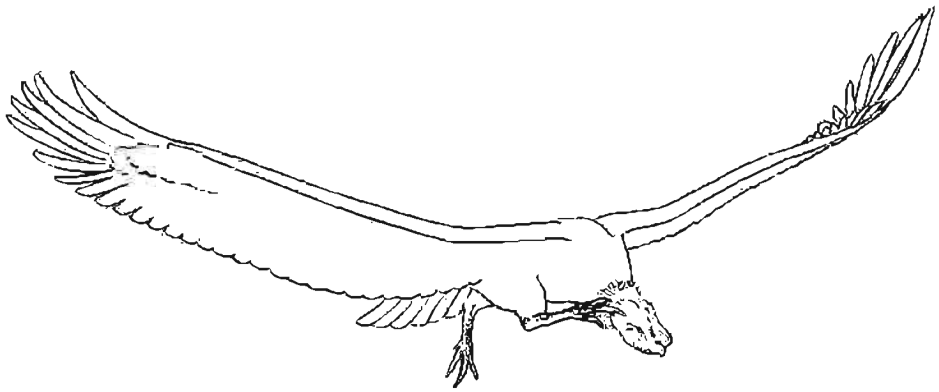


Figure 7. An adult male condor scratching his head in gliding flight.

Simple shaking movements were spaced regularly through quiet periods when the condors were otherwise inactive. During 11 periods when head shaking was apparent, I counted 1 to 11 shakes/min, with a median of 4, for intervals that ranged from 2 to 28 minutes.

I was often irritated by biting black flies (Simuliidae) during these observations; head shaking by the condors may have been a response to these insects. A captive immature male condor shook his head like the wild birds whenever insects landed on his head. During periods of head shaking, wild condors usually had the collar ruff raised to the chin, possibly another response to flies.

Another motor pattern that often accompanied periods of general inactivity was simple head turning. Head turns were slower than movements of shaking and usually did not displace the head as much. Some movements turned the beak through a horizontal arc of up to 90^{o}, but the usual rotation was no more than 45^{o} to 60^{o}. Turning movements were interspersed regularly throughout periods of low activity.

Raising the Ruff

The ruff and the feathers below it can be raised to the base of the skull to cover the neck. Usually associated with a crouched posture, the position was typical of condors standing quietly during cool mornings or during overcast days with cool winds or rain. On occasion, condors exposed to the first rays of the sun on a cool morning did not dun but stood with collars raised. Perhaps, in a sunning posture, head loss to the cool air would have been greater than that gained from the radiant energy of the sun. Maintaining the ruff in the raised position might also reduce heat loss from a naked and exposed neck. On cool days, condors standing around a feeding site sometimes held the ruff in the elevated position. When these birds began feeding, the collar dropped to the neck base; this movement probably prevented soiling of the feathers. Koford

(1953, p. 28) reported that the California condor tended to raise the ruff when temperatures were below 18^{o} C; if the wind blew, the raised position occurred at higher temperatures. He also noted that alarmed condors often raising the ruff. I did not record any association between this response and a state of alarm for Andean condors.

Gaping, Panting, and Blinking

Occasionally a condor will extend the neck vertically, tilt the head up, and open the beak for 1 to 3 seconds. If the neck is extended, the head is usually lifted up to an angle of 30^{o} to 45^{o} above the horizontal. In this gaping pattern, the beak generally opens about 5 cm but may open only 2 to 3 cm. The tongue often moves about during the yawn-like motions, but I was unable to discern any regular movement. Sometimes the tongue was extended to, or slightly beyond, the distal end of the lower beak and then retracted before the beak closed. Often it remained in the posterior part of the beak during the gape. I once saw it lay motionless in the usual mid-beak position. Condors were observed gaping in both lying and standing postures.

Occasionally condors were seen breathing rapidly with the beak open. Watery fluid ran, sometimes profusely, from the beak and nostrils, possibly an exudate from salt glands, for a white residue often remained after evaporation. I saw both immature birds and adults, mostly females, pant, usually after feeding while standing off to the side of the feeding area. Panting seems important in temperature control.

During all wakeful moments the nictitating membrane of the condor appears to flash across they eye frequently. Six frequency values taken at different times and situations on a captive condor ranged from 18 to 28 per minute, with a median of 22. An adult male, perched near his nest, blinked 18 and 20 timer per minute. Values recorded during moments of inactivity at feeding sites were higher, 68 per minute for an immature male, 40 and 34 per minute for an

adult female on a windy beach. Blinking rates of the nictitating membrane obtained for the California condor by Koford (1953, p. 28) and translated to my terms are equivalent to 12 to 30 per minute.

The outer lids close when condors sleep. Frequently, when the bird is preening or wiping its head in sand, the outer lids are closed for short durations.

Vocalizing

I never heard and loud sounds made by wild condors. Hissing was the sound I noted most frequently. When I approached a male nestling 5 to 6 months of age, he made a series of hisses. Each unbroken sound was 4 to 6 seconds in duration and separated from the next by a pause of less than 1 second. His beak was open only about 5 mm at the end, and the tongue was extended forward with the tip beyond the distal end of the lower mandible. Fighting adults hissed similarly. ON several occasions in the Cerro Illescas, adult condors landed above me and hissed.

A captive immature male frequently made a deep rattling sound about 1 second long. The soft but staccato sound resembled air rushing out of a balloon nozzle and probably was produced in an analogous manner. This sound typically preceded a food-begging motor pattern or occurred during a side stretch. When I gathered the bird in my arms, he often made this sound. Apolinar (1914) reported that a captive condor chick 3-weeks-old produced sounds similar to those of mice.

Captive condors in courtship activities often produce clucking sounds (Janda, 1938 ; Protielje, 1949 ; Poulsen, 1963 ; Gailey and Bolwig, 1973). I watched a captive adult female assume a courtship posture in the presence of an adult male and make soft clucking sounds. Although I witnessed numerous courtship interactions by wild birds, I was unable to detect any

vocalizations associated with them. I was usually too far from the condors, however, to hear sounds of low amplitude. Smith (1970) reported low croaking noises from a pair of perched king vultures just after he had flushed one of them from a nest and egg.

Exploratory Nibbling

I saw adults and immature birds of both sexes nibble and play with various inanimate objects. Grass, twigs, feathers, hair, dirt, clam shells, and algae were nibbled at and sometimes carried about in the beak. Anchored twigs and grass were the most commonly used items in short nibbling bouts that usually lasted only a few second. Manipulating objects with the beak is also a common pattern with the California condor (Koford, 1953, p. 29). A captive adult male Andean condor observed by Gailey and Bolwig (1953) pushed straws, sticks, and feathers into the feathers under his wing; these objects fell to the ground after he released them with his beak.

RESPONSE TO WEATHER

Sunning

Description

The condor in a sunning posture extends its wings and usually orients the dorsal surface toward the sun (Plate 11). Generally, the manus and forearms are completely extended so that the leading edge of each wing is nearly straight. Depending on the position of the sun, the angle formed by the axis of the wing chord and the ground varies so that usually the dorsal wing surface is perpendicular to the sun. In early morning observations, the angle between the ground and the wing chord axis was near 90^{o}, while the angle between the horizontal and the long axis of the body was approximately 60^{o}. During midday, the wing-chord axis of sunning condors was

Plate 18. An immature male condor and two black vultures sunning.

usually parallel to the ground, while the long axis of the body formed an angle of about 30^{o} with the horizontal. Sunning black vultures displayed a similar orientation to the sun. While sunning, the condor neither expands the tail completely nor compresses it tightly. The tail is always held parallel to the long axis of the body. Near the end of the sunning bout, the extended manus often descend slowly to positions about 45^{o} below the leading edge of the forearm. Such movements usually precede termination of the sunning posture.

On only a few occasions did I observe condors in a sunning position with the ventral surface of the wings exposed to the sun. Once after bathing, an adult pair, sunning first with their backs to the sun, both turned simultaneously to face the sun, their wings still extended. In the former position, their flight feathers were blown about by the wind; this may have prompted the change in orientation. Occasionally a nestling condor sunned with the ventral surface oriented toward the sun. Koford (1953, p. 26) reported that the California condor sunned the dorsal surface about twice as frequently as the ventral surface. With the Andean condor, it appeared to be at least 10 times as frequent.

Preening usually preceded and followed sunning but occasionally occurred during the sunning bouts, when it was restricted to feathers of the breast, neck, upper back, and the wing coverts. At feeding sites condors occasionally walk or turn around while sunning. I sometimes saw wingbeats interspersed within sunning bouts at feeding and bathing areas but never at the roost. Both wings moved simultaneously and in a direction parallel to the ground. The body was erect.

Social Context.

Condors often sun together. I frequently saw groups of birds of similar or different age and sex classes sun at the same time and place. Although condors often sunned at the same general time, in the morning or after rains, groups often began and ceased at nearly the same

instant, which suggests social factors contributed to the timing. Koford (1953: 26) noted a similar synchrony in sunning patterns of California condors. Sunning usually occurred at roost sites or on perches nearby and less frequently at feeding, bathing, and nest sites. At sunrise, condors often flew together from roost ledges in shaded areas to perches in the sun and remained there until the onset of foraging; they did not always sun on these perches.

Durations.

Adult condors tended to sun for longer durations than younger birds. In Colombia, differences in the sunning durations of nestling and immature condors were not significant, but combined these durations were significantly less than those of all adults[1] and specifically of two adult pairs (Figure 8).[2] Sunning durations did not differ significantly between male and female condors nor between adults in Peru and adults in Colombia. Most durations were 100 to 150 seconds. Differences in durations recorded at different times of day were not significant.

Function.

Expression of the pattern was clearly related to sun exposure. Seven times I saw condors immediately assume the sunning posture when exposed to direct sunlight previously shielded by clouds or fog. On eight occasions, I saw condors cease sunning directly after fog or clouds obstructed direct sunlight. Twice when low fog intermittently shielded direct sunlight, the manus of one adult condor sagged, so the primaries touched the ground during the shaded periods. The manus were instantly re-extended upon each new exposure to the sun. The close relation between the expression of this pattern and sun exposure is similarly marked with *Gymnogyps* (Koford, 1953, pp. 26-27). In Colombia, when could cover was tree-quarters or more, only 5 of 28 sunning durations recorded were greater than 150 seconds, while 28 of 61 durations recorded lasted more 150 seconds during clearer skies.[3] Fewer long durations of direct exposure to the sun on cloudier days probably account for the shorter bouts. Sunning did occur,

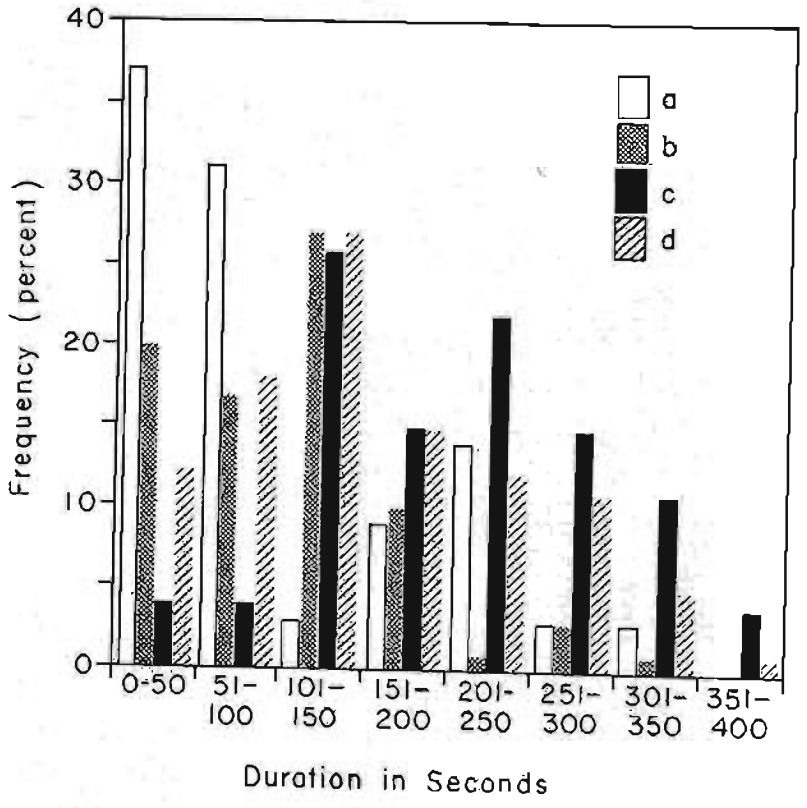


Figure 7. Frequency of sunning durations. a. nestling and immature condors in Colombia (n=35); b. pair 1 in Colombia (n=30); c. pair 2 in Colombia (n=27); d. adult condors in Colombia and Peru (n=74).

however, in a few instances when condors were not exposed to direct sunlight.

I searched for other clues to the function of sunning by comparing differences in sunning behavior between a nesting and a non-nesting pair. Sunning timetables and durations for members of pairs 1 and 2 were significantly different between but not within pairs (Table 3).[4] Durations for the nesting pair (2) were longer and occurred earlier in the day. Although the proportion of early-hour observation time for members of pair 2 was slightly higher than that of pair 1 (about 2.5 percent; see total observation time values for pre-forage periods and the remainder of the day listed in Table 16), the difference does not appear large enough to explain the difference.

If sunning functions in warming or drying, then earlier bouts might be protracted to obtain effects similar to those later in the day. The additional feeding pressure on adults caring for a large feathered chick might demand greater, and consequently earlier, foraging efforts. Maintenance activates like sunning might also occur earlier. Yet in all of the four observations where the onset of foraging by both pairs could be clearly established, the non-nesting pair 1 left the roost earlier. I was unable to determine if this sequence of departure was a consistent pattern. I made no other timetable comparisons for sunning because I was unable to compensate for variations in total observation time for different hours of the day.

The average rate of sunning observed for either member of pair 1 was about one occurrence for every four condor-hours of observation time for either of the two birds; for pair 2, the rate was about one occurrence for every six condor-hours (an hour of observation time when both members were observed is figured here as two condor-hours). I tested for differences in the two rates by comparing observed frequencies of sunning with expected values (27.5 for pair 1, 43.5 for pair 2) generated from the total observation time on members of each pair from Tables 16 and 19 . Differences between the rates were not significant.

Table 3. Sunning timetables. A tally of sunning observations made in Colombia classified by the time of day.

Hour	Percent of sunning bouts observed during hour listed											Total no. observations
	0600-0659	0700-0759	0800-0859	0900-0959	1000-1059	1100-1159	1200-1259	1300-1359	1400-1459	1500-1559	1600-1659	
Pair 1	0	23	34	6	3	23	6	3	3	0	0	35
Pair 2	0	25	44	25	3	0	0	0	0	3	0	36
Immature condors	0	0	0	0	42	33	8	8	0	8	0	12
Female nestling	0	0	9	43	13	26	9	0	0	0	0	23

Although the pattern is related to sun exposure, the precise function of the posture is not clear. Perhaps the most obvious possibility is the use of solar energy to raise the body temperature thus conserving the condor's own energy. Several observations on a captive immature male condor appear to conflict with this hypothesis. In 5 of 10 instances when sunning occurred within intervals between two cloacal temperature readings the second temperature recorded was less than the first. All intervals between readings were 30 minutes or less. The cloacal temperature may not be a reliable indicator of changes in the temperature of the body core or of some other specific part of the body.

Several additional observations also seem to undermine the idea of a warming function. In one case, the captive bird sunned after an extended period of leaping and flapping; the cloacal temperature before sunning was a relatively high 40.60^{o} C. The cloacal temperature dropped over 1^{o} C by the second reading, after the bird had sunned. This young bird almost always stood in a sunning posture following a bath, suggesting a feather-drying function. Once, he panted while standing with wet, outstretched wings.

While observing wild birds from a blind in the Cerro Illescas area, I saw an adult female leave the bait and sun for 105 seconds. The ambient temperature was about 30^{o} C, and the condor seemed quite warm, for she panted throughout the sunning bout and defecated on her tarsi both just before and just after the bout. Here, the sunning posture may have acted as a communication signal; a sub-adult female also fed at the bait. After walking from the carcass, the adult turned and jumped back towards the bait and suddenly assumed the sunning posture. The sub-adult also took up the sunning posture for the same duration. After folding her wings, the adult returned to the carcass and fed while the sub-adult looked on.

Grier's (1973) study of sunbathing in a number of different bird species, the Andean condor and turkey vulture among them, found little evidence to support the idea of temperature

control; his experiments and observations tended to support the idea of feather drying as the function of sunning.

Perch Use and Sun Exposure

In the observations at the roost area of pairs 1 and 2, I noted that the adult condors appeared to seek perches exposed to the sun during the early morning hours but avoided sun-exposed areas later in the morning and day. To obtain a measure of this apparent attraction and avoidance for different hours of the day, I monitored the use of 24 perches, recording whether those used were exposed to the sun by virtue of topography when (1) cloud cover was less than 75 percent, or when (2) it would have been if it had not been cloudy (cloud cover greater than 75 percent, Table 4). Records of perch use when skies were predominantly clouded provided base-line data (the null model) for comparison with data when skies were more open. If perch selection depended on daily stimuli related to sun exposure, then for periods when condors were attracted by direct rays of the sun, I expected to find sun-exposed perches under a relatively open sky used more often than when the sky was obscured by clouds. And conversely, for those periods when exposure to the sun was avoided, perches exposed under an open sky probably would have been used relatively more often during hours when skies were predominantly cloudy, compared to those periods with a more open sky.

Data recorded on both the duration and frequency of occurrence of perch use appear to bear out these relationships (Figure 9). Between 0700 and 0900, sun-exposed perches were used more often when cloud cover was less. From 0900 to 1000, a shift occurred so that from 1000 to 1300, perches in position for sun exposure were used less often during hours when cloud cover was less. Sunning observations for these two pair fit well with relationships obtained here. The 2-hour period when these four birds appeared to be attracted by the sun accounted for more than

Table 4. Cloud cover and perch use by pairs 1 and 2 in Colombia. Data recorded on 28 days from 28 November 1968 to 29 January 1969 for instances of perching that were 1 min or more in duration. The nest site and perches around bathing areas were not included among the 24 perches observed. Cloud cover values recorded hourly.

	Time of day													
	0500-0559	0600-0659	0700-0759	0800-0859	0900-0959	1000-1059	1100-1159	1200-1259	1300-1359	1400-1459	1500-1559	1600-1659	1700-1759	1800-1859
Cloud cover < 75 percent														
-Sun-exposed perches														
Total no. min perched	0	1	855	972	321	146	101	127	23	43	40	0	0	0
Total perching occurrences	0	1	34	53	24	8	8	5	1	2	2	0	0	0
-Perches not exposed to sun during hour listed														
Total no. min perched	58	558	201	107	197	205	362	276	340	642	518	900	788	324
Total perching occurrences	5	15	15	10	22	17	20	15	26	32	25	42	56	21
Cloud > 75 percent														
-Perches that would have been exposed to sun if it were cloudless during hour listed														
Total no. min perched	0	0	108	280	272	130	106	23	0	0	2	50	0	0
Total perching occurrences	0	0	4	11	7	7	8	4	0	0	2	2	0	0
-Perches that would not have been exposed to sun even if it were cloudless during hour listed														
Total no. min perched	98	806	412	172	107	49	68	42	42	134	359	414	426	209
Total perching occurrences	7	16	15	8	7	5	9	3	8	10	16	26	26	10

There's some duplication with this table and Fig. 8, but the material is complex enough, I think, to warrant separate treatments. Without this table it would be difficult to explain the derivation of Fig. 8. (J. McGahan)

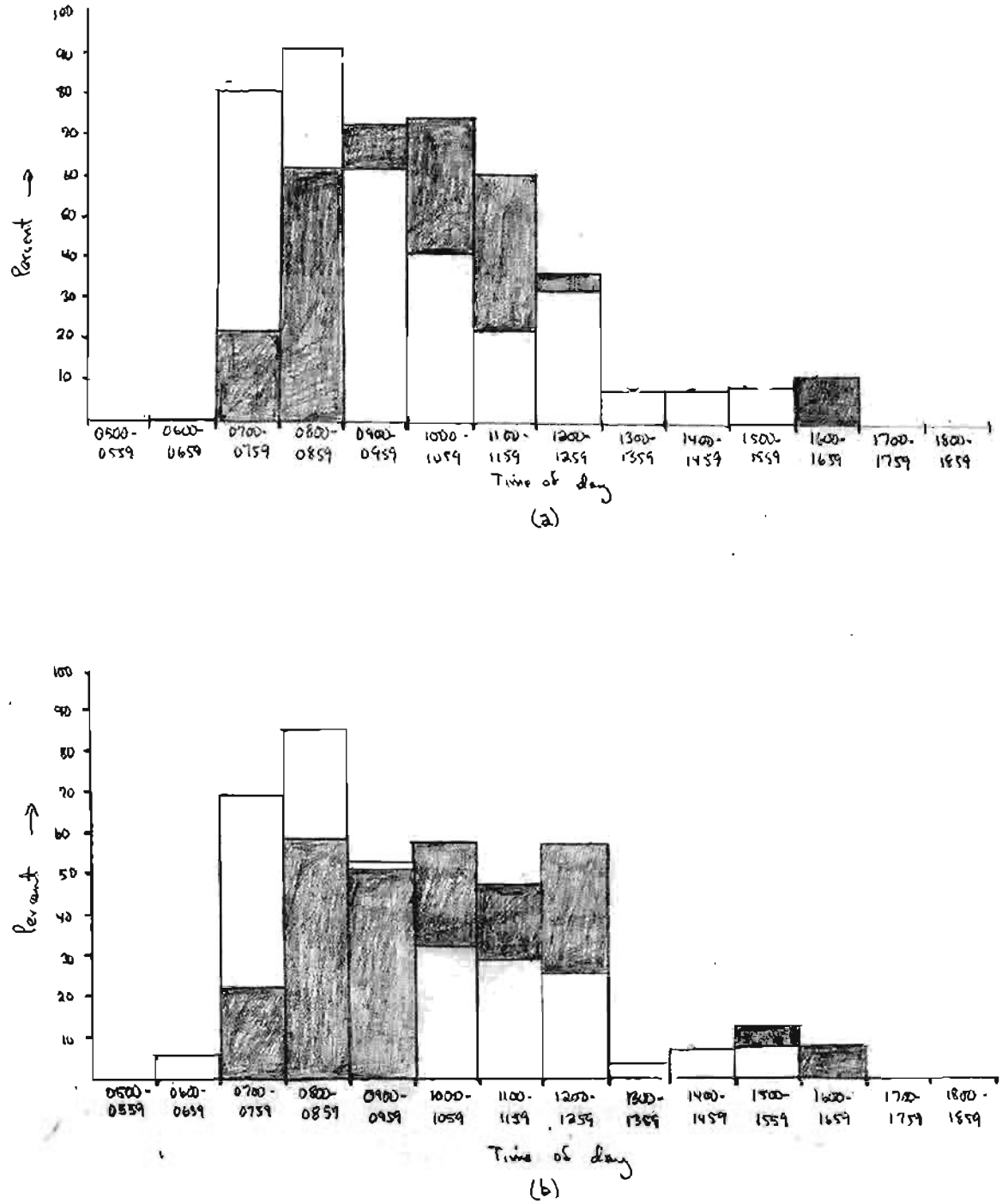


Figure 9. Percent of (a) total time and (b) total number of perching occurrences on perches that were or would have been exposed to the sun during cloudless periods. Observation time cloud cover was less than 75 percent is represented by open bars and observation time when cloud cover was greater than 75 percent by shaded bars. See Table 4.

half of the sunning bouts observed (Table 3).

Few perches used by any of these condors were exposed to the sun during the afternoon hours, so attraction-avoidance comparisons were hampered for that period. Condors probably avoid sun exposure during the afternoon hours when air temperatures are maximum; the presence of afternoon shade probably played a role in the selection of this area as a nesting and roosting location.

After bathing during midday periods, condors went to perches exposed to the sun. On the three occasions when condors were observed bathing, only sun-exposed perches around the bathing area were used, all of them during cloudless periods from 1000 to 1400. In these instances, a total of 300 minutes was recorded for time on sun-exposed perches. I never saw a condor bathe on a cloudy day or stand in the shade during the half-hour period that followed a bath.

In the Paracas study area, where cold winds blew off the ocean, condors were usually seen on sun-exposed perches throughout the day. On this coastal area, daily temperatures were often 3^{o} to 5^{o} C less than those in Colombia. All of the condor roosts on the coast faced directly toward the afternoon sun; in the morning condors often left these ledges and flew around points to east-facing cliffs and perched there in the sun until the wind came up. At one roost where there were no east-facing cliffs nearby, the condors sometimes flew up to the top of the cliffs and stood in the sun on the hills of sand above.

Foraging and Air Movement

Condors seem to be incapable of sustained flight in still air (see Chapter 8), so foraging apparently depends on air that is in motion. This direct relation between the foraging activity of

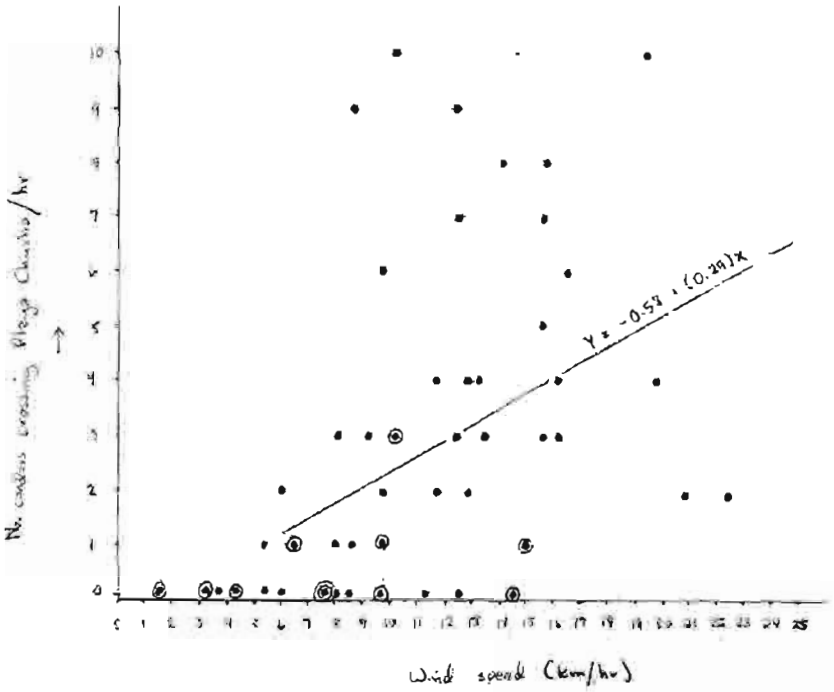


Fig. 10. Foraging activity related to wind speed. The number of conures crossing Playa Chucita hourly was recorded daily from 1 January 1990 to 12 January 1990 within the period from 0630 to 1500. Mean values for wind speed were computed from half-hour readings on anemometers supported by a 5-m tower that stood in the center of the beach ($n = 59$; $r = +0.47$; $p < 0.01$).

condors and wind conditions was evident on a Paracas beach, Playa Chucho (Figure 10). Relative measures of population activity along the linear foraging routes of the coast were easily obtained by recording the number of condors crossing Playa Chucho each hour. For each increment in wind speed of 10 km/hr recorded, an average of approximately three additional condors were observed gliding across the beach. Because wind speed was closely related to the time of day, the correlation with wind speed might simply be a consequence of the diurnal fluctuations of some other primary stimulus. I examined the data for this possible effect by computing partial correlation coefficients. Variation in population activity could not be explained by any of the variation in time of day when wind speed was held constant. On the other hand, 38 percent of the variation in population activity could be attributed to variation in wind speed when time of day was held constant. Hence, the primary stimulus for the activity recorded did seem to be the wind (Figure 10).

Similar data were difficult to obtain in Colombia, where representative measures of air movement were not easily secured. On the Paracas coast, condor flight seemed powered most often by cliff-deflected winds that blew from the sea, so the strength of vertical currents was probably a fair reflection of the speed of the steady wind measured at Playa Chucho. In Colombia, where both local and large-scale thermal movements acted together over irregular terrain, I was unable to obtain a direct measure of the air conditions important in the flight of condors.

Another indicator I measured, however, did seem closely related to the flight characteristics of air. Examining the relationship between canyon fog and roost departure by pair 1, I found that foraging began later when fog was more prevalent in the roost area. This relation suggested that the onset of foraging was limited by the stillness of air, represented in a direct fashion by the prevalence of fog (Figure 11). Late departures from the roost probably did

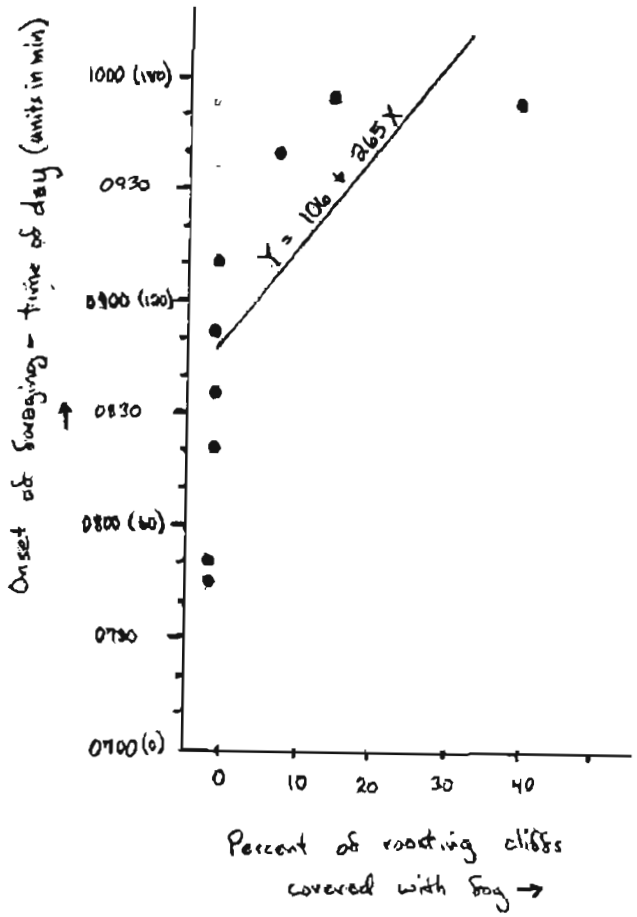


Fig. 11. The onset of foraging by pair 1 related to fog conditions in the roost area. Data recorded from 7 December 1968 to 15 February 1969 ($n = 9$, $r = +0.72$, $p < 0.04$).

not depend on reduced visibility because the fog usually remained below the canyon rim in an area not often crossed by the first morning routes of foraging. In sum, observations on weather and foraging activity support contentions made in the analysis of flight that the mobility of condors depends largely on air movement (Figure 11).

Rain

The response of both adult and nestling condors to rain was mixed. Usually, they seemed to avoid rain, but at other times they appeared to seek it out. Both young and adult condors often stood, sat, or lay in caves or back under the protection of an overhanging rock when it rained. On three separate occasions, I saw an adult fly from an exposed perch and land on a sheltered ledge when it began raining. Frequently, however, adults remained perched on exposed sites when rain began to fall. Several times, I saw adults flap their wings during exposure to the rain. The axis of movement by the wings was horizontal and seemed no different from the wingbeats made sometimes by condors just after bathing. Davis (1970) observed wing flapping by turkey vultures perched in the rain; she also cites several instances when these smaller vultures moved to the protection of rocks or heavy vegetation during rain. McKelvey (1965) saw a flock of 14 turkey vultures depart from the protection of living trees to open snags, where they stood in the rain with open wings.

Twice, I saw condors visit the Colombain baits and feed during rain. One adult male, at the bait for 16 minutes, fed without pause even though thunder sounded and rain fell continuously for 8 minutes. The rain ceased before he flew.

Temperature Control

Activities described earlier like panting and defecating may be important in temperature

control. I made a series of cloacal readings on the captive condor and recorded the frequency of certain activities between readings. The condor responded well to this inquiry and usually allowed me to introduce and anal thermometer 4 or 5 cm into his cloaca repeatedly for 3-minute periods.

Panting.

Panting may have served to cool this bird. High respiration rates were significantly associated with high cloacal temperatures. In 11 observations when the cloacal temperature was less than 39.5^{o} C), the respiration rate was less than 50 cycles per minute, whereas rates for 3 or 4 readings made at higher cloacal temperatures ($\geq$ 39.5° C.) were 50 cycles per minute or more.[6]

In one 3-minute period, I saw the captive condor change abruptly from a panting rate of 70 cycles/min to 30 cycles/min and then repeat this pattern once; clouds momentarily obscured the sun during the two intervals with reduced rates of respiration. Most panting rates were around 60 to 75 cycles/min, whereas respiration rates in the dozing state dropped as low as 11 cycles/min. The highest rate of 100 cycles/min was recorded after a period of struggling when I restrained the bird for a series of measurements. On a hot day after feeding, one adult female stood panting, her wings slumped out to the side with the wrists about 30 cm from the body, a posture that might facilitate cooling. In another instance on a hot day, an adult female panted each time she raised her head during a feeding bout (Plate 19).

Defecation on the Tarsi.

Defecation on the tarsi apparently serves as a mechanism for cooling. Evidence for this hypothesis has been presented for storks by Kahl (1963) and for turkey vultures by Hatch (1970). This common trait supports the idea that storks and New World vultures are closely related (defecation on the tarsi has not been reported for any of the Old World vultures). Data

Plate 19. Adult female condor panting during a pause in feeding on a Burmeister's porpoise.

recorded for this behavior from the captive condor also indicate a function of cooling. In 9 hours of observation, this bird deposited white matter on the right tarsus and foot 15 times and on the left tarsus and foot 16 times. The sequence of deposition moved from one tarsus to the other with significant regularity.[7] When fecal material was not present in the excrement, deposition on the ground and the tarsi was equally frequent in 34 observations, whereas excrement containing fecal material observed in 25 instances always fell to the ground. This relationship, a significant one,[8] indicates that the condor actively avoided depositing fecal solids on the tarsi. As the rate of elimination increased, the most frequently used site of deposition appeared to change from the ground to the tarsi and feet (Table 5). Although the choice of deposition site seemed unrelated to cloacal temperature I found that the tarsi or feet were used more frequently at higher ambient temperatures (Table 6). Todd (1974) noted a direct relation between frequency of the pattern and ambient temperature for a captive *Gymnogyps*.

In summary, then, the captive vulture frequently applies wet, white matter of excrement on the tarsi and feet but avoided depositing fecal solids there. The bird regularly alternated from one tarsus to the other and tended to use the tarsi more often than the ground at higher ambient temperatures. The idea that evaporation on the tarsal skin functions to cool the bird appears consistent with these observations, although it should be noted that I found no relation between frequency of the pattern and cloacal temperature. Protection against parasites seems unlikely; I found no macroscopic parasites frequenting clean tarsi but did notice a number of Hymenoptera insects visiting tarsi coated with white excrement.

Correlates of Cloacal Temperature.

Cloacal temperatures of this bird tended to be significantly higher when the condor was exposed to a sunny rather than a cloudy sky, both in Peru and Colombia (Table 7).[9] I found no

Table 5. Deposition site of defecation by a captive immature male condor classified by the rates of elimination for 18 1-hr. observation periods.

Defecation rate	≤6 patterns/hr	>6 patterns/hr
Preferred site of deposition (used for at least 2/3 of the instances)		
On ground behind feet	0	15
On tarsus or foot	2	1

$p<0.04$, Fisher test

Table 6. Deposition site of excrement classified according to cloacal and ambient temperatures. Data from a captive immature male condor.

	Percent readings at cloacal temperature listed (C°)				Total no. observations
	38.00-38.49	38.50-38.99	39.00-39.49	39.50-39.99	
Deposition site					
Ground	21	50	21	8	24
Tarsi or feet	20	60	20	0	5

	Ambient temperature		
Deposition site	<20°C.	≥20°C.	
Ground	22	2	$p<0.05$, Fisher test
Tarsi or feet	2	3	

Table 7. Cloacal temperatures (°C) of a captive immature male recorded in different contexts. Data from 21 days of sampling. Statistical treatments at 0.1°C level.

	Percent of readings at temperature listed									
	37.8-38.0	38.1-38.3	38.4-38.6	38.7-38.9	39.0-39.2	39.3-39.5	39.6-39.8	39.9-40.1	40.2-40.4	>40.5
Activity during 15- to 30- min period preceding temperature reading										
Inactive	2	15	24	20	17	12	10	0	0	0
Preening, streiching, shaking	4	4	19	33	19	15	4	4	0	0
Walking, running, flapping	3	8	14	17	11	28	0	11	3	6
Wind speed-Paracas										
≤8 kph	0	27	10	20	17	20	7	0	0	0
>8 kph	0	6	24	35	12	12	6	6	0	0
Sun exposure										
Paracas										
Sunny	0	14	8	27	16	22	8	3	3	0
Cloudy	0	29	29	14	29	0	0	0	0	0
Colombia										
Sunny	0	0	7	13	27	27	7	13	0	7
Cloudy	0	8	50	33	0	8	0	0	0	0

relationship with wind speeds but I did find a significant relationship with activity of the bird during the 15- to 30-minute period preceding the temperature reading. Cloacal temperatures following periods of walking, running, or flapping were significantly higher than those following periods when the condor was inactive or involved in relatively quiet activities like preening, stretching, or body shaking.[10] Five of the six cloacal temperature readings that were over 40^{o} C followed periods of active movement. The highest temperature, 41.62^{o} C, was taken after the condor struggled to escape while he was being restrained for a series of measurements. I found no relationship between the level of activity and exposure to the sun; these two variables seem to be independent of each other. For readings made in Paracas after periods of inactivity 30 minutes or longer, I found no significant relationship between the cloacal temperature of this condor and either the ambient temperature (Table 8)[11] or the hour of the day.[12] Yet, in a similar comparison with Colombian data, I found significant relationship with cloacal temperatures and both the ambient temperature[13] and the hour of the day.[14]

To determine the independent effects of these two variables, ambient temperature and time of day, I computed partial correlation coefficients for reading from the hours of 0300 to 1500. Because the method describes only linear relationships, I excluded the two readings made after 1500; from 0300 to 1500 the relationship between ambient temperature and time of day would be more linear than that including late afternoon periods, when daytime temperatures begin to drop. By holding the time of day constant, I found that only 1 percent of the variation in cloacal temperature could be explained by variation in the ambient temperature. When I held ambient temperature constant, however, I found that 27 percent of the variation in cloacal temperature could be accounted for by changes in the time of day.

The condor apparently responded to some stimulus to stimuli, other than ambient temperature, that fluctuated regularly according to the time of day. Perhaps the amount of light

Table 8. Cloacal temperatures (°C) of a captive immature male condor recorded after periods of inactivity 30 min or more in duration. Data from 21 days of sampling.

Colombia			Paracas		
Hour of day	Ambient temperature	Cloacal temperature	Hour of day	Ambient temperature	Cloacal temperature
3	19.0	37.95	6	14.0	39.74
6	18.7	38.45	7	15.5	38.80
6	19.6	38.52	7	15.2	38.43
6	19.1	38.37	7	16.3	38.89
6	18.9	38.56	7	16.3	38.69
8	20.2	38.58	7	16.5	39.51
8	20.4	38.82	8	16.0	38.86
9	20.5	38.89	8	17.3	39.17
9	22.0	38.90	8	18.0	39.12
10	22.9	38.45	8	19.5	39.23
10	23.3	40.14	9	19.0	39.70
11	24.7	38.84	9	20.5	38.65
12	25.0	39.79	9	19.5	39.75
12	25.2	38.99	9	20.8	38.20
13	26.0	39.37	10	18.0	39.02
13	26.1	38.64	10	24.5	39.11
13	26.2	39.12	10	18.8	38.41
13	27.2	39.52	10	20.5	38.31
14	26.7	39.37	10	19.7	38.18
15	28.5	39.36	10	20.0	39.31
19	22.0	38.97	10	20.0	38.94
20	21.8	38.69	10	21.0	38.19
			10	22.0	38.19
			11	21.0	38.56
			11	22.5	38.18

was one such stimulus; this might explain depressed temperatures at night as well as those recorded under cloudy rather than sunny skies. Another possible factor might have been the duration of inactivity. At night, temperatures dropped (5-10^{o} C) and periods of inactivity extended into the hours; temperatures rose during the day at the same time that the bird became relatively more active. Perhaps the relationship between time of day and cloacal temperature would have been insignificant if all readings had been taken after periods of inactivity that were 1 hour or more in duration. If early morning readings had been taken in Paracas a similar relationship between cloacal temperature and time of day would probably have appeared.

To sum up then, I found evidence that defecating and panting serve to cool the bird, while sunning in condors seems to have some function other than warming, perhaps feather drying. Cloacal temperatures fluctuate regularly according to time of day, a positive relationship to light perhaps, or a reflection of activity levels.

Germane to the topic of temperature control is a suggestion by S.A. Mahoney (Duke University, pers. comm.) that flight itself may be one of the simplest and most effective forms of cooling. In general, during the daytime periods with the highest temperatures, ground level will be the warmest location. Cooler temperatures occur at higher altitudes, with the scale of difference approximated by the adiabatic lapse rate. Perched condors that prefer to cool themselves may choose flight as a means of encountering lower ambient temperatures, and do so at an airspeed that accelerates heat exchange if it exceeds wind speed at the perch.

DIURNAL VARIATIONS IN ACTIVITY LEVELS

The frequency and duration of some patterns were related to certain stages or segments of the diurnal activity cycle. To clarify some of these differences, I divided that data from 114 30-minute observation periods into three groups, representing the main segments of the daily cycle,

and analyzed them for differences in activity levels. The first segment, the pre-foraging period, comprised all morning observations of condors before the onset of foraging activity. The last segment, the post-foraging period, included all observations of condors that had returned to the roost area for the night. All other observation periods were included in the midday segment. Generally, the periods fell clearly into one of three discrete segments, but occasional overlap did occur. I did not group data according to specific times of day, because discernible changes in condor activity seemed to be more consistently related to when foraging activity commenced and ended than to specific times of day. Thus, the latest pre-foraging period began at 1030 and the earliest midday at 0845. In the afternoon, the latest midday period began at 1530, whereas the earliest post-foraging period began at 1452.

Preening activity varied markedly among the diurnal periods. Condors preened almost half of the observation time during the post-foraging segment and less during the other segments (Table 9). In two other comparisons midday preening bouts were characteristically brief. Although the fraction of them preening for pre-foraging and midday segments was similar, the frequency of preeing bouts in midday segments was significantly greater. In the second comparison, preening time during the post-foraging segment was longer than that during midday, but the frequency values were similar.

During the pre-foraging segment, condors sat or lay for one quarter of the total time. Later in the day, the fraction of time spent in these rest postures decreased. The amount of time condors sunned also decreased as the day progressed. I never saw condors sun during the post-foraging segment. During midday, condors seen sunning usually had just bathed.

Simple frequency distributions for two patterns, stretching and short flights, were notable. Almost all stretching behavior was restricted to the pre-foraging segment, a tendency also noted for the California condor (Koford, 1953, p. 27) and turkey vulture (Davis, 1974). The Andean

Table 9. Activity levels of some motor patterns during different segments of the day.

	Pre-foraging segment	Midday segment	Post-foraging segment
Number of 30-min observation periods	57	44	13
Part 1			
Mean and computed standard error for number of minutes/30-min observation period in which activity occurred			
Preening	8.6 ± 1.5	8.4 ± 1.3	13.2 ± 2.7
Sitting or lying	7.6 ± 1.5	3.2 ± 1.4	1.6 ± 1.4
Sunning	0.6 ± 0.2	0.3 ± 0.1	0
Part 2			
Percent of 30-min observation periods in which activity occurred			
Preening	51***	89	92
Sitting or lying	42***	11	15
Sunning	19	14	0
Bow stretching	18*	2	0
Side stretching	23***	0	0
Short flights (perch to perch)	7**	32+	8

\+ $p<0.10$
* $p<0.05$
** $p<0.01$
*** $p<0.001$

Determined by applying chi-square test or Fisher test to raw data. When a notation is absent between values of adjacent columns, the null hypothesis could not be rejected at the 0.10 level. No tests applied to data in Part 1.

condors I watched made more short flights to various perches in a single area during the midday period than at other times.

Diurnal variations in the activity of ther patterns probably exist but are difficult to assess. Determining significant differences in the level of activity for relatively rare patterns requires an enormous amount of observation time. Statistical treatments for data on rare events are not very powerful.

SEQUENTIAL ORGANIZATION

I used a stochastic analysis of behavior observations to detect sequential associations of behavior patterns of the condor. First, I assembled records of successive patterns into a contingency matrix and then tested it to determine if the number of joint occurrences of antecedent and successive patterns departed significantly from the number expected on the basis of individual pattern frequencies. Major departures indicate relations in the sequence.

Method of Study

This analysis assumes the data source is stationary, that is, the transitional probabilities remain constant over the sampling period. In reality, various irregularities may have violated this assumption: (1) I pooled data on many condors during different periods and assumed that all behaved similarly with respect to the sequence of patterns. (2) in the preceding section, the frequencies of some different behavior patterns are seen to vary with the time of day; transition probabilities may fluctuate as well; (3) differences in age and sex are not considered; (4) observing condors in the Colombian Andes and on the Peruvian coast, I ignored different habitat factors. The small sample size in this study restricts analysis to two patterns at a time and

neglects possible processes or organization that depend on longer chains of antecedent behavior. Despite these problems, the sequential organization appears marked and consistent enough so that the analysis is thought to contribute to the understanding of condor behavior. Supporting evidence exists in the similarity of some sequences that I have noted for the condor with those of the skylard, *Alauda arvensis*, as reported by Delius (1969) .

For behavior patterns described in this chapter, I recorded 593 transtion dyads (or pairs of patterns in sequence) and divided these dyads into two groups according to the duration of the interval separating each pair. Dyads separated by intervals less than 1 minute are presented in Figure 12, and those separated by intervals exceeding 1 minute are presented in Figure 13. Rows represent antecedent patterns and columns successive patterns. Because a pattern interrupted by short intervals could be considered arbitrarily as either a single pattern or many short ones in a sequence, categories with a pattern succeeding itself were deleted in Figure 12 . Except for preening, where the problem was critical, only one observation of another category (head scratch) was deleted (Figures 12 and 13).

To compare observed with expected frequencies for each category or cell, I compressed the remainder of the matrix and performed a two-sample chi-square test. Categories with substantial departures ($X^2 \geq 3.84$) were designated with frames of heavier lines and the direction of deviation noted. Although this technique provides a convenient means for comparing associations, two limitations must be kept in mind: (1) With the X^2 value computed in each test, one can make a probability statement about the chances of that occurrence considered alone against the compressed matrix. It is not possible, however, to use these X^2 values in formulating probability statements about two or more tests simultaneously in a single matrix, because each individual probability is dependently related to the others. Thus, departures considered significant alone are termed here simply as substantial in the multiple comparisons. (2)

Precede \ Follow	Bow stretch	Side stretch	Defecation	Body shake	Preen	Head scratch	Take off	Others	
Bow stretch		1.47 0	0	0.15 1	0.87 10	0	25.61 + 14	9.37 − 0	25
Side stretch	46.65 + 10		3	0.12 1	0.07 7	0	3.42 1	4.12 − 2	24
Defecation	2	0		0	1.01 5	0	2	0.35 2	11
Body shake	6.80 + 5	0.08 1	1		3.02 4	0	5.66 + 9	0.48 5	25
Preen	1.06 6	3.85 + 10	1.36 2	9.04 + 13		5.15 + 7	0.18 23	45.57 + 57	118
Head scratch	1	4	0	1	0.45 3		1.01 1	0.06 3	13
Land	4.93 − 0	3.53 0	2.19 0	1.83 1	38.07 + 37	2.00 0	1.33 7	2.00 10	55
Others	4.94 − 2	0.27 4	3.56 6	0.58 4	25.21 + 50	0.61 4	5.35 − 10	5.76 − 16	96
	26	19	12	21	116	11	67	95	367

Figure 12. Dyad frequencies for transitions between motor patterns separated by intervals less than 1 min. Chi-square values are listed for those transitions with an expected frequency exceeding one. Substantial departures (chi-square equal to or greater than 3.84) are framed with heavy lines, and the direction of departed is noted. Based on 93 hr of observation.

Precede \ Follow	Sit or lie	Stand up	Preen	Take off	Other	
Sit or lie	0	8	7.81 − 0	2.06 0	2.76 0	8
Stand up	2	0	1.63 1	0	0.65 2	5
Preen	5.72 − 0	11.75 − 0	6.26 + 52	0.18 17	0.01 23	92
Land	1		0.19 7	1.28 1	0.29 4	13
Others	0.00 1	2.86 0	23.51 − 6	5.63 + 13	0.00 10	40
	4	8	76	31	39	158

Precede \ Follow	Neck	Breast	Back	Left side and wing	Right side and wing	Tail	
Neck	3.96 + 11	1.10 8	0.07 4	0.39 9	4.68 − 7	1.95 0	39
Breast	0.22 7	1.36 3	3.04 1	3.78 11	0.36 13	1.72 0	35
Back	0.43 3	0.14 3	0.11 3	0.03 5	0.28 9	0.00 1	24
Left side and wing	0.04 7	0.05 6	1.07 3	2.41 12	0.15 13	0.06 2	43
Right side and wing	1.80 10	0.19 13	4.61 + 14	8.72 − 7	2.33 31	0.37 4	79
Tail	0.00 1	1	1	1.49 0	0.72 1	2	6
	39	34	26	44	74	9	226

Figure 13. Top: dyad frequencies for transitions between motor patterns separated by intervals greater than 1 min. Based on 93 hr of observation. Bottom: dyad frequencies for transitions between different preening sites on the body separated by intervals less than 1 min. Treatment of top and bottom same as in Figure 12.

Departures are designated by tests providing X^2 values larger than 3.84 ($P < 0.05$, 1 *df*), hence, in a random system with no associations, an average five out of every 100 tests will specify a substantial departure.

Results and Discussion

Patterns Separated by Brief Intervals.

Examination of the matrix in Figure 11 shows that bow stretching and preening were the patterns most frequently associated sequentially with other patterns. For the skylark, bow stretching was the pattern most often associated with other (Delius, 1969). A side stretch by the condor usually preceded a bow stretch; the reverse did not occur. Apparently the two patterns were similarly related with the California condor (Korford, 1953, p. 27). In the skylark, however, both sequences of the stretching pattern appeared more often than expected. In *Vultur* and in the skylark, the bow stretch often followed a body shake. Vultur usually bow-stretched or shook the body before flying and usually preened after landing. Similarly, *Gymnogyps* frequently bow-stretched before flying and preened after landing (Koford 1953, p. 30). Davis (1974) noted that side stretching, body shaking, and other wing movements often preceded flight by the turkey vulture.

With *Vultur*, preening tended to precede a number of comfort movements: the body shake, head scratch, and side stretch. Delius (1969) suggested feather displacement by preening provided the stimulus for a body shake. Among the behavior patterns listed in Figure 11 , preening was unique in its positive association with the pooled group of other activities. This relationship may be due to social factors; earlier, I noted preening as an important activity in social settings. The other individual patterns listed in Figure 12 may have a more consistent

relation with functions of body maintenance or comfort.

Patterns Separated by Extended Intervals.

Transition dyads for patterns separated by intervals exceeding one minute are listed in Figure 13. Diagonal categories provide no problem in this matrix since fixed minimum intervals separate without ambiguity instances where a pattern follows itself. Across these longer intervals, preening followed itself more than expected on the basis of individual frequency. Delius (1969) noted the same result for the skylark. A lack of discernible activity by condors that have been sitting or lying for at least 1 minute is obvious from the data in Figure 12 . Preening does not precede standing up nor sitting or lying nor does it succeed sitting or lying. After a bird sat or lay down for 1 minute, the only subsequent activity I noted was standing up again.

Preening.

In another stochastic analysis I assembled a matrix of 226 dyads describing preening movements from one part of the body to another. Movements separated by pauses no greater than 1 minute were recorded and the transition frequencies listed in Figure 13 . Preening in the neck area seemed to succeed itself. Condors appeared to move from the right side and wing to the back but tended to avoid movement from the right side to the left. Delius (1969) reported that the skylark also appeared to move from one side to the other less often than expected. Few frequencies depart from those expected, which suggests that the selection of an area for preening by the condor is largely unrelated to the location of the antecedent preening site (Figure 13).

CONCLUSIONS

For a number of behavior patterns and postures by birds familiar to most observers, the function remains unknown. In search of clues to the purpose of some of these patterns, I examined the context of their appearance by recording which activities occurred before and after a certain pattern or posture, the time of day, certain weather conditions, and, in some instances, the social situation. A clear relation found between behavior and setting may clarify what the behavior does for the bird.

Preening apparently serves the obvious role of feather maintenance; the behavior often occurs after foraging, in general, and flight, in specific, and is associated sequentially with other body maintenance patterns. A common appearance in social situations also suggests some kind of signal role. Stretching precedes activity, occurring early in the day and often just before flight. Perhaps this movement serves as a kind of muscle "warm-up" or maybe alters, in some fashion, the tonus pattern of nerve-muscle activity to prepare for an exertion. Body shaking tends to precede flight and follows preening, which indicates a role in feather arrangement. Head wiping almost always follows feeding; with this pattern, condors cleaned their necks and head of food material and blood.

Weather correlates presented the strongest evidence for the function of certain behavior patterns. Sunning behavior was clearly related to sun exposure and, except for instances following bathing, usually occurred in the morning. Observations on the sunning behavior of a captive bird and records of cloacal temperature suggested that sunning did not serve to warm the bird but rather to dry the feathers. Sunning patterns figured in social contexts and might also have served some communication role. Two Colombian condor pairs sought sun exposure on their perches in the morning from 0700 to 0900 but avoided it after 1000. The early 2-hour

period accounted for more than half the sunning bouts recorded for these four birds. In the Paracas area, where a cold wind was a prominent feature and average temperatures ranged from 3^{o} to 5^{o} C less that in Colombia, condors appeared to seek the warmth of sun exposure throughout the day.

Foraging movements are closely allied to air movement. Observations in two study areas with completely different wind conditions both describe this relationship. On one Peruvian beach, an average of about three additional condors per hour glided across it for each increment of 10km/hr in the wind. Condors in this area use vertical air currents produced by the upward deflection of horizontal winds by coastal cliffs and hills. In Colombia, where most vertical air currents are probably thermal in nature, roost departure in the morning tended to occur earlier on days when air movement was greater. Limitations of flight when wind speed is very low or nil are treated in more detail in Chapter 8.

Condors frequently defecate on their legs and feet as do some other New World vultures and storks. This peculiar pattern, along with panting, may cool the bird. Evaporation on the skin of legs and feet and inside the beak probably helps in ridding the body of excess head. Both patterns occurred at greater frequencies when ambient temperatures were high ($> 30^{o}$ C). Panting often occurred at cloacal temperatures exceeding 39.5^{o} C. A captive condor avoided depositing solid fecal matter on tarsi and feet, and applied instead only the wet, white matter. Application alternated from one tarsus to the other on a regular basis. Raising the collar ruff on the neck appears to help conserve head during cool periods. High cloacal temperatures correlated with time of day and may reflect a direct relationship with light or an indirect relationship with activity.

CHAPTER 4. REPRODUCTION

INTRODUCTION

The major objectives of this chapter are a determination of the timetable or calendar for reproductive events, an understanding of pair bond maintenance, and the isolation of key behavior patterns in organizing the activities of two parents and their offspring.

Because of the latitudinal extent of the Andean condor's range, nesting dates can vary markedly from Colombia to southern Chile. The California condor normally breeds only every other year if the juvenile survives (Koford 1953, p. 87), whereas Andean condors may have breeding cycles of one year, two years, or even 18 months. The first part of this chapter deals with latitudinal variation in dates of the nesting season and its possible effect on duration of the breeding cycle.

Pair bonds of the Andean condor seem to extend beyond the nesting season. Two male-female pairs of adult condors roosted on one series of cliffs in the Colombia study area; one pair was nesting and the other was not. Thus, from one observation point, I could examine the effects of breeding status on mate associations and relations and daily foraging timetables. Both pairs experienced the same general climatic conditions, not only over large-scale foraging areas but in the same small roosting area. The availability of food should have been comparable for both pairs. In this situation, I was able to ask questions such as: Do nesting condors spend more, or less, time foraging than non-nesting birds? Do nesting mates spend more time with each other at the roost, or at foraging, than non-nesting mates? What effects do chick rearing seem to have on the frequency of courtship and copulation patterns? Because the sample size in this examination is a minimum, however, differences noted for the two pairs may reflect individual nature more than breeding status. This possible shortcoming must be kept in mind.

Courtship and copulation behavior by the non-nesting pair in Colombia and by condors

observed in Paracas, far from possible nesting areas, suggest that sexual activity cements a pair bond that endures beyond the period of nesting. Sexual activity seemed to occur whenever condors were observed in groups for extended periods; hence I was able to record information on a large number of courtship and copulation patterns. Part of this chapter examines evidence for the extended pair bond and considers its adaptive value. I looked at the setting of the different courtship and copulation patterns and considered the effects of time of day and year, location, and, of course, the social situation. I searched for fixed sequences of motor patterns, beginning with courtship and ending with copulation, to determine what patterns seemed necessary for completion of the full courtship-copulation sequence. Extended observation at two different nests allowed me to see whether both parents shared equally in the task of rearing the chick, if chicks were fed only at certain times, the relation between the frequency of chick feeding and proximity of food, and how adults apportion food to themselves and to the chick. The last section of this chapter concerns the behavior of nestlings. Here, I provide a compendium of behavior patterns, along with a number of daily timetables for resting, flapping and leaping activity, sunning, and use of the cave interior.

THE TIMETABLE

In the more temperate and seasonal zones of the southern latitudes from about 20^{o} S to 50^{o} S, condors apparently begin nesting during the spring, around October. In the equatorial Andes of Colombia, the period of nesting may vary widely (Table 10). Pairs 2 apparently began nesting in April and pair A in October, in nests that were less than 1 km apart. Egg laying coincided with the rainy periods. Harsh winter conditions that might harm an egg or chick are absent in equatorial areas, but seasonal variations in food availability could affect the reproductive timetable. In contrast to condors of the Colombia study area, black vultures there

Table 10. Dates of egg laying for different latitudes.

Location	Estimated laying date[a]	Source of data
Near Pasto, Columbia Lat. 1°29'N	April, 1968	Nestling 2
Near Pasto, Colombia Lat. 1°29'N	October, 1969	Nestling A
Cordillera Real, Bolivia Lat. 14°-22°S	August-October, 1864	An egg taken on 4 October, 1864 by W.A. Worthinson-San Bernardino Co. Museum
Near Vallenar, Chile Lat. 28°-29°S	October, 1932	Partially feathered male chick taken from nest by William Millie on 23 April 1933 (pers. comm.)
Near Santiago, Chile Lat. 33°-34°S	October-November, 1870	An egg taken by R.A. Philippi on 30 November 1870 - Smithsonian Institution
Near Santiago, Chile Lat. 33°-34°S	September-October, 1951	An egg taken in October, 1951 for R.A. Philippi-Western Foundation of Vertebrate Zoology
Rio Gallegos, Argentina Lat. 52°S	October-November, 1904	A partially feathered chick taken on 18 March 1904-Adams (1907)
South American Andes	August-October, 1888	An egg taken on 17 October 1888 for Rev. C.M. Phelps-San Bernardino Co. Museum

[a] Estimates obtained allowing 56 days for incubation and six months from hatching to the fully feathered stage.

appeared to nest at only one time of the year. We saw parents feeding young at the baits only from July to November even though the smaller vultures continued to frequent the baits into March of the following year.

Species differences in reproductive timetables could depend on the extent of parental dependency by the juvenile. I was unable to follow the activities of the Volant juvenile and parents long enough to determine the duration of dependency for the Andean condor. For black vultures, the period may be as long as 6 months (Jackson, 1975). Koford (1953, p. 87) estimated a period of dependency of up to seven months for volant juvenile *Gymnogyps*. This period extends beyond the egg-laying season of the following spring. Thus, California condors apparently are limited to nesting successfully once every two years if the juvenile survives, although F.C. Sibley has reported successful annual nesting for four consecutive years by one pair (Mertz, 1971). Even if Andean condors must accommodate this prolonged juvenile dependency, they might be able to nest twice every three years in equatorial zones, where climatic variation is not extreme.

Several observations suggest, however, that the period of dependency by the volant juvenile *Vultur* is shorter than that of *Gymnogyps*. I rarely saw adults with volant, dependent juveniles. Of the many interactions recorded for adults with young during the two years of field work, I saw a volant juvenile being fed by an adult only three times. These observations were made during one 3-day period in the same area near La Paz, Ecuador; presumably, only one juvenile was involved. If periods of juvenile dependency by *Vultur* are as extended as those of *Gymnogyps,* adult-juvenile relations should have been more apparent. In another situation, two immature males that fed and foraged independent of any adults (IM2 and IM3) may have been less than a year old. The beaks of both birds were completely black. Grey patches appeared on the sides of the beak of the captive immature condor by the time he was 12 months of age. If

changes in the beak color occurred at the same rate for IM2 and IM3, they probably had been independent of parental aid for less than six months after leaving the nest. A dependency period of four months or less could permit adults to breed annually, assuming an incubation of two months and na nestling period of about six months. Possibly, Andean condors breed annually in both equatorial and temperature zones.

SEXUAL BEHAVIOR

Courtship

Courtship behavior is considered here as the activity commonly associated with sexual activity by the male and female. Such activity probably functions to affix the pair bond and to coordinate sexual and nesting timetables for successful reproduction. Behavior like social nibbling and preening was not restricted to relations between birds of the opposite sex. This broader setting implies a function that is not sexual. These and other motor patterns that were common but not characteristic of male-female relations are dealt with in Chapter 5. In contrast, one commonly seen stance occurred rarely unless adults of both sexes were present; the courtship posture preceded every apparent copulation that I saw.

Description of the Courtship Posture.

A condor in the courtship posture extends both wings, stands erect, and arches the neck so that the head is pointed downward (Figure 14a). The leading edge of the extended wings is not straight as it is in sunning positions. Wrist and elbow are slightly flexed so that the wrists are elevated to a level above the base of the neck (Figure 14b). The primary feathers of sunning birds are approximately horizontal, but they point downward in courtship to form an angle of 30^{o} to 60^{o} with the horizon. Koford (1953, p. 77) noted a similar difference in courtship and sunning postures of the California condor, as did Davis (1979) with the turkey vulture.

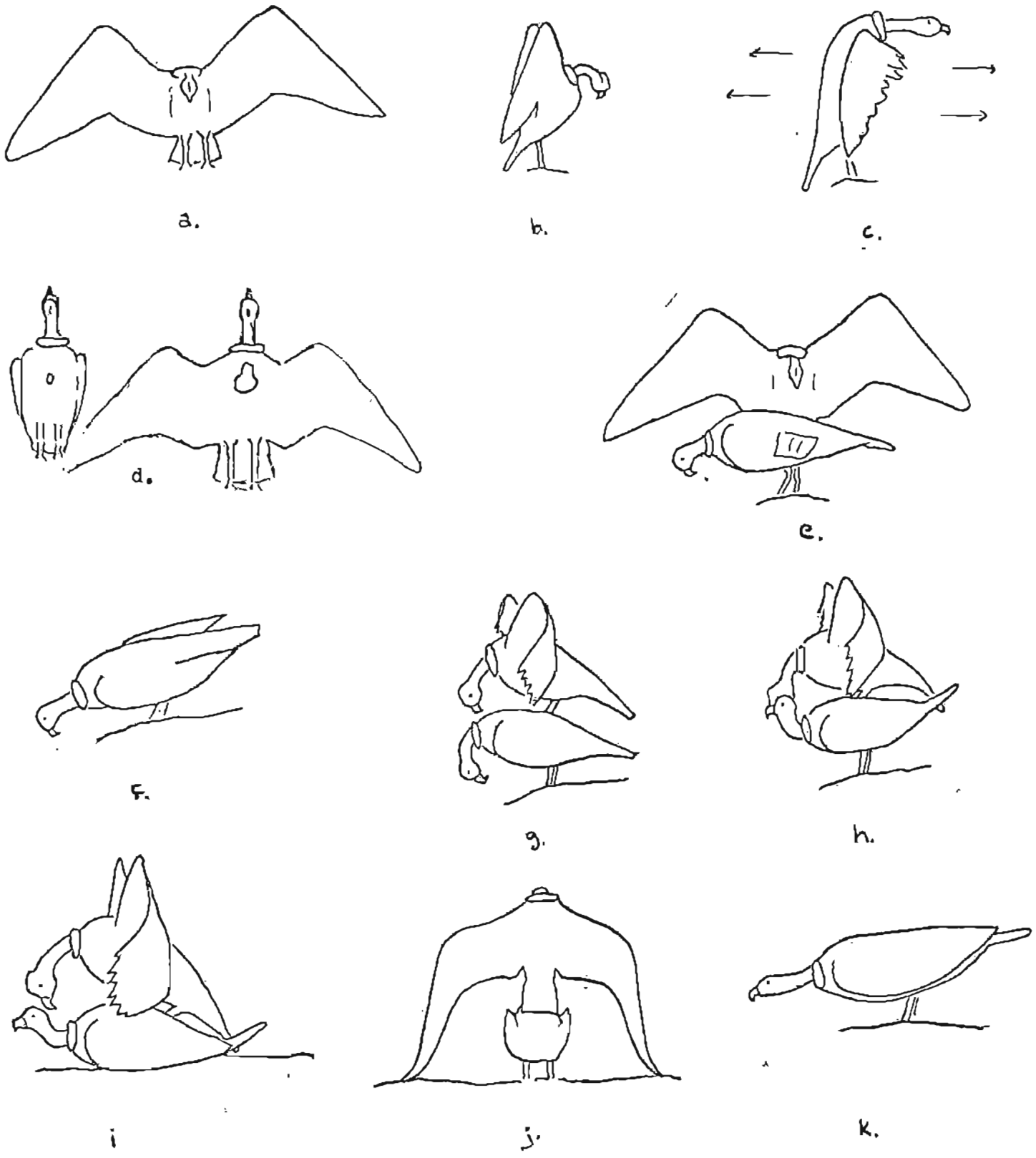


Figure 14. Courtship and copulation postures. a-f postures in courtship; g-i three stages of one copulation sequence; j another copulation posture, k side view of the female position in j.

When the wings extend to the courtship position, the neck arches and the head descends until the beak points toward the ground, with the top of the head presented forward. Occasionally, the head did not bow until several seconds after the wings were extended. When the courtship posture ends, the head ascends to a normal position, either while the wings are being folded or just afterward. A difference in head and neck position between sexes was not apparent. Turkey vultures do not lower their heads in the posture (Davis, 1979).

With *Vultur* birds of either sex may initiate courtship. When the pair perched together, the condor courting usually faced the partner, although the courting birds frequently shuffled about, turning from side to side (Figure 15). In 16 of 25 bouts by males, the courting bird turned across arcs ranging from 60^{o} to 2.5 full circles. In four bouts, the male shuffled ahead several steps; in the remaining five bouts, I saw no shuffling. For female bouts, turning occurred in 9 of 11 recorded, shuffling forward in one, and no movement in one. In one posture, AM1 turned two full circles in about 12 seconds. AF1 flapped sometimes as she turned about in courtship. In one period of courtship, she flapped her wings about 80 percent of the time that she paced back and forth in front of the male; sometimes only the wing facing her mate moved.

Vocalizations may be typical of the courtship posture. An adult female courting in captivity vibrated her throat flap in rhythm with a soft clucking sound emitted at a rate of four to five per second. Portielje (1949) and Poulsen (1963) reported a similar sound made by captive males in courtship, but Whitson and Whitson (1969) failed to detect it in the courtship they observed, although they did note a "low moaning sound" from the female during copulation. Gailey and Bolwig (1973) noted a number of audible sounds by a captive pair in courtship and copulation patterns; hissing by the male typically preceded the courtship posture, whereas guttural clucking characterized the posture. The female made a continuous groaning sound that ceased when copulation ended. Then both birds often hissed simultaneously after the male

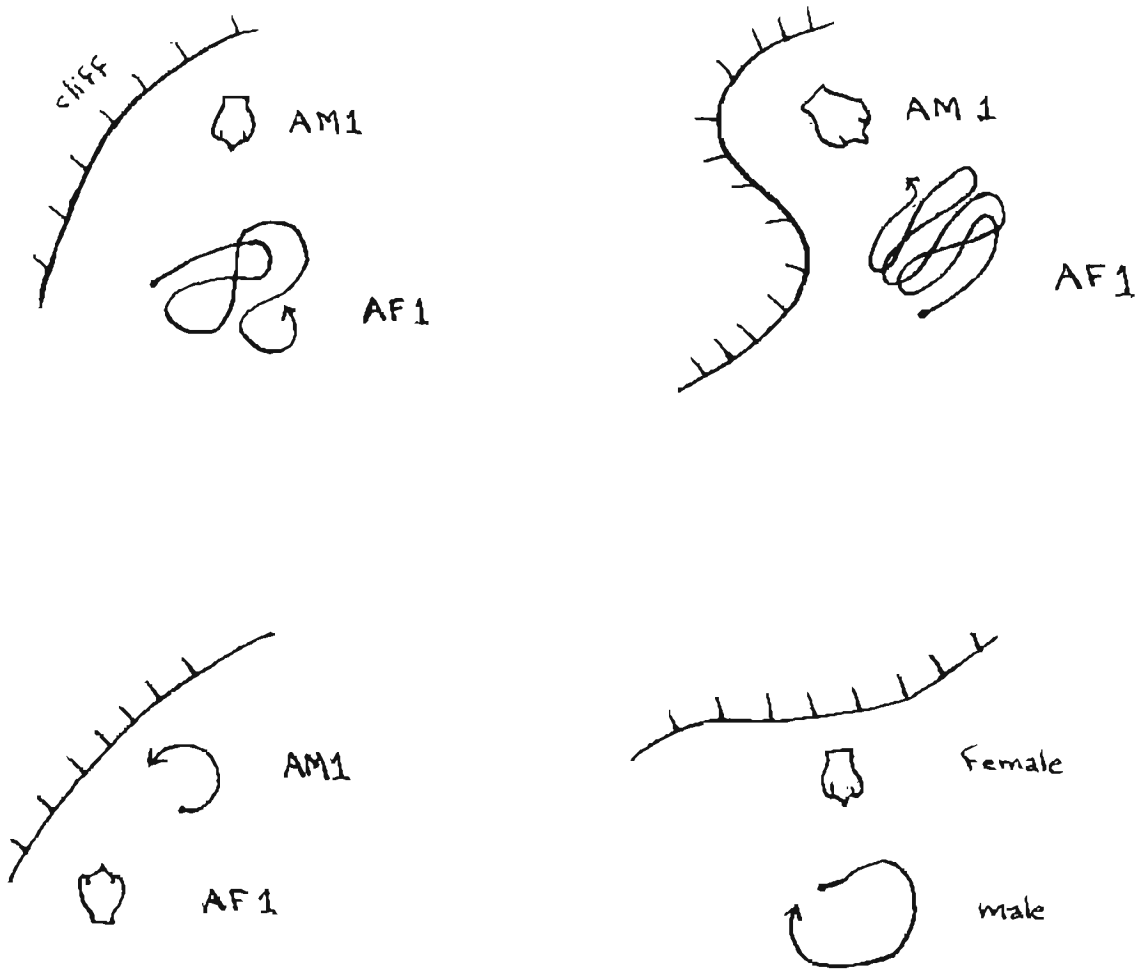


Figure 15. Walking and turning movement during the courtship posture. Point of arrow represents the front and the direction of movement of the courting bird. Top view. From the Colombia study area.

dismounted. Because of distance, I could not determine whether any sound or throat motion characterized courtship bouts or copulation in nature.

In 15 instances of courting by adult males I noted an expansion of the crop area, an effect apparently produced by inflating air just beneath the skin. The area of naked skin exposed increased markedly (Figure 14d). The skin of the inflated neck area of birds courting in captivity apparently changes in color toward a more intense red and yellow (Portieje, 1949; Poulsen, 1963; Gailey and Bolwig, 1973). I noted no change in crop appearance of courting females. If expansion of the crop area occurs in the female courting posture, its expression is probably less noticeable or less frequent or both. Crop areas of both male and female, however, were sometimes seen expanded during aggressive encounters

Male-Female Variation.

Courtship by females was less frequent than that of the males and sometimes markedly different in form. Of 78 separate bouts of posturing, males performed 50 or 64 percent, a significantly greater number.[1] Wing movement during courtship seemed characteristic only of females. I recorded data on wing motion according to sex for 60 courting bouts and obtained the following results: The extended wings did not move in all 12 bouts recorded for AM1 and in all 14 bouts for other males but did move in 17 of 26 bouts by AF1 and in 4 of 8 bouts by other females. Sex-associated differences for presence of wing movement by pair 1 was significant.[2] In sum, I noted flapping in 21 of 34 female courting bouts and none in 26 bouts by adult males. Amplitude of the wingbeat by a courting female was not markedly different from that of a bird in flight; speed of movement ranged from one to two wingbeats per second. Wrists and elbows usually remained partially flexed throughout the full cycle. A slight pause in motion marked the end of each recovery. Action of the wingbeat often resembled that of a begging chick. Occasionally, the wingbeat seemed no different than that of a flying bird, except that the axis of

motion was horizontal.

Durations.

I recorded durations for the courtship posture when I saw both the onset and end of the pattern (Table 11). Durations ranged from 1 to 120 seconds, but most were short; about half of those recorded were 10 seconds or less. AF1 tended to remain in the posture longer than her mate.[3] The median value for observed postures by AF1 was 28 seconds and for AM1 5 seconds. In a similar comparison for other males and females, durations did not vary significantly nor did they in the comparison for AM1 and AM2. Courtship postures observed for turkey vultures lasted only a few seconds (Davis, 1979). Condors often assumed the courtship posture repeatedly during a single short period. For example, AM1 once assumed the courtship posture five times for durations of 5,3,4,20, and 4 seconds, with separating intervals of 1 to 3 seconds.

To obtain an interval value for defining an individual bout of courtship posturing, I plotted, against interval duration, the logarithm of the cumulative frequency of intervals between courtship patterns by a single bird (Figure 16). A straight-line distribution in this kind of analysis approximates that of an exponential decay function and implies that the probability of an event ending is constant across the time period considered. Angle of the slope represents this probability with steeper slopes indicating that intervals tend to be shorter. Concave curves occur when more short intervals occur than expected whereas convex curves occur with a relative preponderance of longer intervals. This method of analysis is described in more detail by Hailman (1974).

Intervals between instances of courtship plotted in this manner show that the probability that another posture would follow was greater during the first minute than in the interval following. Since the greatest change in slope occurred at the 1 minute interval, a single bout was considered as any series of individual instances separated by intervals less than 1 minute (Figure

Table 11. Durations recorded for the courtship posture. Data from all three study areas.

		Percent of courtship postures observed with following duration (sec)						
	Median (sec)	1-2	3-5	6-10	11-30	31-60	61-120	Total no. observations
AM1	5	7	53	7	27	7	0	15
AM2	16	17	11	22	33	17	0	18
Other adult males	5	42	17	8	25	0	8	12
AF1	28	6	6	12	38	19	19	16
Other adult females[a]	12	0	25	12	50	12	0	8

[a] No durations recorded for AF2.

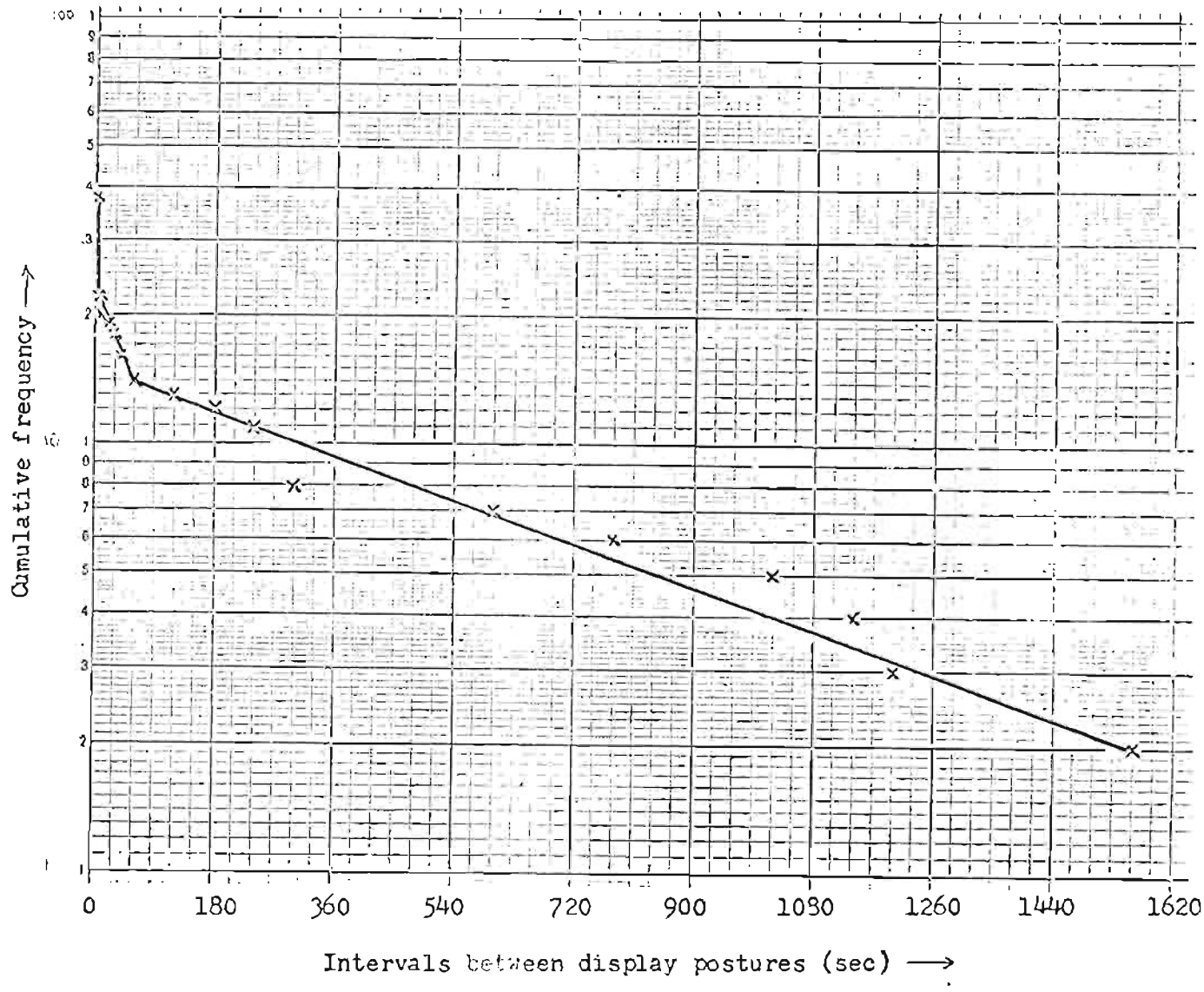


Figure 16. Logarithms for the cumulative frequency of intervals between courtship patterns by a single adult condor plotted against duration of the interval *(n=38)*. Separate graphs constructed for males and females were similar, so the data were combined.

16 and Figure 13).

Stimulus and Response.

As inferred by the name courtishp posture, a necessary context is the presence of an adult member of the opposite sex. That context did characterize 104 courtship postures observed; the few exceptions noted are considered later. The apparent targets of courtship activity were usually perched nearby (89 percent of the instance observed), although sometimes they were flying, usually above the bird courting (Table 12). On three occasions, the flying condors landed near the courting bird but no other sexual activity followed immediately. Rarely did both members of a pair court simultaneously. Courtship terminated immediately when the other mate took off.

Condors apparently being courted responded differently (Table 13). Although the non-nesting AF1 responded with courtship or copulation postures in 9 of 17 intervals following mate courtship, the nesting AF2 made no apparent sexual response at all to 18 courtship bouts by her mate. The difference in response was significant.[4] AF2 frequently remained perched in a normal posture when her mate courted; sometimes she flew and he immediately resumed a normal stance. The combined group of other female tended to respond in the same manner as AF1. A similar comparison for response differences between other females and AF1 was not significant but it was with AF2.[5] That difference may have been related to variation inherent in the individual birds or to a difference in the reproductive status; unlike other condors in the comparison, AM2 and AF2 were caring for a nestling at the time. Koford (1953, p. 78) observed that courtship was rare with nesting *Gymnogyps*.

Female courtship may often be important in the sequence of patterns leading up to copulation although it seems to be less so in the interval immediately before copulation. A male was never observed to mount a female directly after she courted (Table 13). In contrast, male

Table 12. General activity of the condor apparently stimulating courtship by another. Data from all three study areas.[a]

Courting bird	Percent observations that the bird apparently being courted was involved in the following activity:[b] Perched	Flying	Flying then perched	Total observations
AM 1	93	3	3	30
AM 2	74	22	4	23
Other males	95	0	5	20
AF 1	92	8	0	24
Other females	100	0	0	7
			Total	104

[a] With four exceptions not considered in this table (see p. 92), all birds apparently acting as a stimulus for the courtship posture were adults of the opposite sex.

[b] AF 1 courted by AM 1; AF 2 by AM 2; and AM 1 by AF 1.

Table 13. Response to courtship. Specific activity by the bird apparently being courted, for the period of courtship and 5 sec following. Data from Colombia and Peru for pairs perched within 10 m of each other.

	Percent observations for following responses by bird apparently being courted.[a]				
	Sexual posture				
Courtship bout by:	Copulation	Courtship	Nibbling interaction	Stand quietly or take off	Total no. observations
AM 1	35	18	0	47	17
AM 2	0	0	28	72	18
Other males[b]	44	0	12	44	16
AF 1	0	38	8	54	13
AF 2	0	0	0	0	0
Other females[b]	20[c]	20	0	60	5

[a] AF 1 courted by AM 1 and v.v.; AF 2 by AM 2.

[b] Data from all three study areas combined.

[c] Female mounted the male (see text, p. 100).

courtship postures were recorded in 12 of 15 intervals immediately prior to copulation. In two of the intervals where the male did not court, the female mounted the male; in each case, she assumed the courtship posture before mounting, once immediately before and the other 7 seconds before. Copulation postures occurred significantly more often after male rather than female courtship (Table 13).[6] If courtship posture by the bird mounting is an important element in the sequence of action prior to copulation, fewer instances of female courtship immediately preceding copulation may be related to the infrequency of females mounting males. According to Davis (1979), turkey vulture courtship by the mate thought to be female is rare.

Time and Location.

Sexual encounters occurred more often during midday periods. I tested for these time-related differences by comparing the frequency of courtship bouts and copulation postures observed for six periods of the day with expected values generated from the total amount of time that pairs were seen together during that period (Table 14). Differences in sexual activity tallied according to time of day did not vary significantly within or between pairs 1 and 2 so I combined these data. Expected values proceed from the assumption that the frequency of events is a function of the total observation time for a given context; that is, fewer events occur in brief periods while more will occur in longer ones. Thus, I obtained values for the expected level of sexual activity by multiplying the fraction of total observation time that pairs were able to court or copulate during each hour by 78, the total number of courtship bouts and copulation postures actually tallied for these two pair. Differences between expected and observed values were highly significant.[7]

To obtain some descriptive measure of sexual sensitivity for different periods of the day, I performed two-sample chi-square tests on expected and observed frequencies for each period after compressing the remainder of the matrix in each test (see p. 69-70). Results presented in

Table 14. Sexual activity and time of day. Data from Colombia study area during 38 full days of observation from 11 November 1968 to 2 March 1969.

	1600-0759	0800-959	1000-1159	1200-1359	1400-1559	1600-1859	Total
No. and percent (in parentheses) courtship bouts and copulation postures observed							
Pair 1	0(0)	15(26)	11(19)	10(17)	12(21)	10(19)	58
Pair 2	1(5)	5(25)	3(15)	7(35)	2(10)	2(10)	20
No. min mates observed <400 m apart[a]							
Pair 1	543	748	491	262	345	759	3163[b]
Pair 2	763	874	303	495	724	861	4257
No. days pair observed together during that time of day							
Pair 1	12	26	18	14	18	33	
Pair 2	15	22	14	18	20	30	

[a] When either one or both mates perched.

[b] Values for time observed together are slightly less here than in Table 16 because, for several observations, pair activity was not discernible, whereas their locations were.

Figure 17 show that sexual activity seemed suppressed during the pre-forage and post-forage periods of the morning and evening and emphasized during the midday (Figure 17).

I found no relationship between levels of sexual activity and time of year for periods from 11 November 1968 to 2 March 1969 (Table 15). Differences in sexual activity monitored during the periods did not vary significantly between or within pairs 1 and 2, so values for both pairs were combined as in the previous test. I treated these data in the same manner as those relating sexual activity and time of day, but the variation examined here was not statistically reliable.[8]

Sexual activity was not restricted to any particular area. I saw courtship and copulation not only on ledges at roosts and nest areas but also on the ground at feeding locations in all three study areas. Only one instance of courtship and an apparent copulation was observed at a feeding area in the Cerro Illescas, but few baits were used there. In the Cerro Illescas, I once saw courtship on a hill that was not in the immediate vicinity of a nest, roost, or food source.

The Courtship Posture as a Threat?

In four isolated instances, a stance similar to the courtship posture seemed to occur in agonistic (fight or flight) contexts rather than sexual ones. In two instances, the posture occurred in aggressive encounters between condors of the same sex: (1) At a bait in Colombia, AM1 landed, ran at AM3, and then assumed a stance similar to the courtship posture in front of the other crouched male (Figure 18). After an exchange of pecking motions, AM1 turned, resumed a normal stance, walked to the carcass and fed while AM3 flew. (2) In the Cerro Illescas, an adult female (#1) displaced another (#2) from a perch. Rapid pecking exchanges preceded and followed a 5-second courtship posture may also have served to threaten a potential competitor, even though aggressive motions were not apparent. (3) An adult male (#2) landed at a carcass on Isla Zárate where another adult male (#1) and an adult female fed. Facing the newcomer, male

Table 15. Sexual activity and the time of year. Data from Colombia study area during 38 full days of observation from from 11 November 1968 to 2 March 1969.

	Time of year[a]											
	11 Nov-24 Nov	26 Nov-29 Nov	2 Dec-7 Dec	9 Dec-16 Dec	17 Dec-18 Dec	19 Dec	20 Dec	21 Dec-22 Dec	23 Dec-27 Dec	28 Dec-31 Dec	2 Jan-2 Mar	Total
No. and percent (in parentheses) courtship bouts and copulation postures observed												
Pair 1	8(14)	6(10)	6(10)	1(2)	7(12)	5(9)	6(10)	3(5)	0(0)	9(16)	7(12)	58
Pair 2	0(0)	0(0)	2(10)	1(5)	0(0)	2(10)	1(5)	2(10)	3(15)	1(5)	8(40)	20
No. min mates observed <400 m apart[b]												
Pair 1	357	239	173	524	309	164	276	338	189	103	491	3163
Pair 2	320	363	466	170	383	423	577	388	360	417	390	4257
No. full days of observation	5	3	3	5	2	1	1	2	2	4	10	38

[a] Periods range from 1-59 days and are divided so that equivalent amounts of condor observation time are obtained for each period. In each period the mates of either pair were observed less than 400 m apart for a total time of no less than 500 min.

[b] When either one or both mates perched.

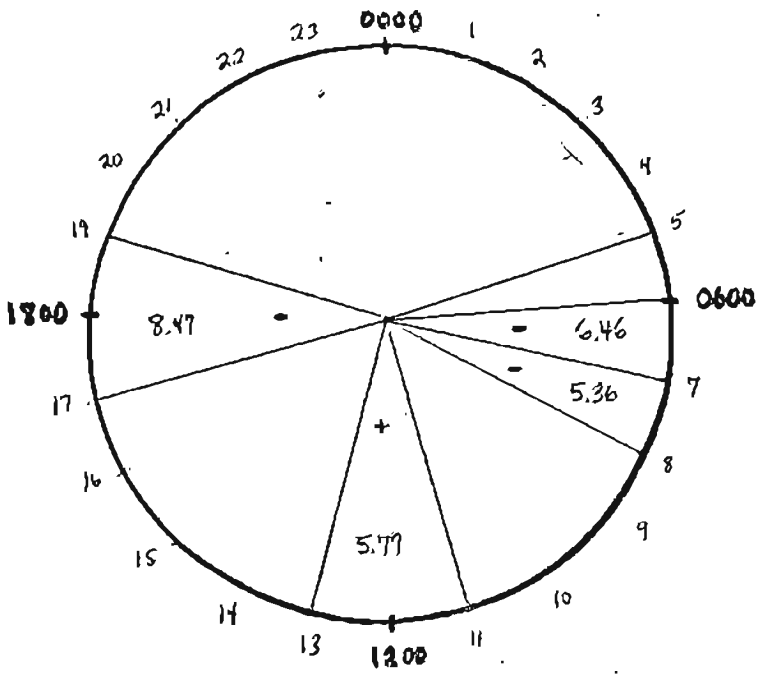


Figure 17. Sexual activity and the time of the day. Observed and expected values for levels of sexual activity from data in Table 14 are compared for different periods of the day. Separate two-sample chi-square tests were performed for each period with the remainder of the matrix compressed. Chi-square values are shown along with the sign of departure for those periods with substantial deviations (with chi-square values equal to or larger than 3.84).

#1 assumed the courtship posture twice, Then, in a normal stance, male #1 approached male #2, and they touched beaks before male #2 backed away. (4) An adult male with full crop jumped down from a ledge on the island and approached an adult female and sub-adult male that fed together. The approaching male assumed the courtship posture for 2 minutes, walking first to the female and then the young male, touching heads for a moment with each bird. Then, when another adult female landed on the beach, the male ceased courting, turned, and chased her.

Koford (1953, p. 80) described a similarity in appearance and context for courtship and threat attitudes by the California condor. Threat postures of the nesting *Gymnogyps* resembled the courtship posture, in that the wrists of partially flexed wings were elevated above the base of the neck; wingtips, however, remained near the body, and the bird did not turn from side to side. These relations hold for the two postures of *Vultur*, as well. Although the arched neck and downward-pointing head were characteristic of both postures for *Gymnogyps*, the neck extended forward in threat postures observed for *Vultur*, both for captive (Poulsen, 1963; Gailey and Bolwig, 1973) and wild birds (Figure 18).

Color changes of the skin and inflation of the neck area by Andean condors occurred in both sexual and aggressive encounters. Gailey and Bolwig (1973) also reported this phenomenon in the two setting by a captive pair; they noted, however, that a ruffling of the scapular feathers appreared only in the threat attitude.

Other Courtship-Related Activities

Social nibbling was often associated with courtship, occurring before and after bouts of posturing by either sex. Nibbling activity preceded 13 of 54 instances of courtship posturing by males (24 percent) and two of 16 instances by females (12 percent). The frequency of nibbling activity observed before courtship was not significantly related to the sex of the courting bird nor did it seem associated with the presence or absence of nibbling after courtship. Mutual nibbling

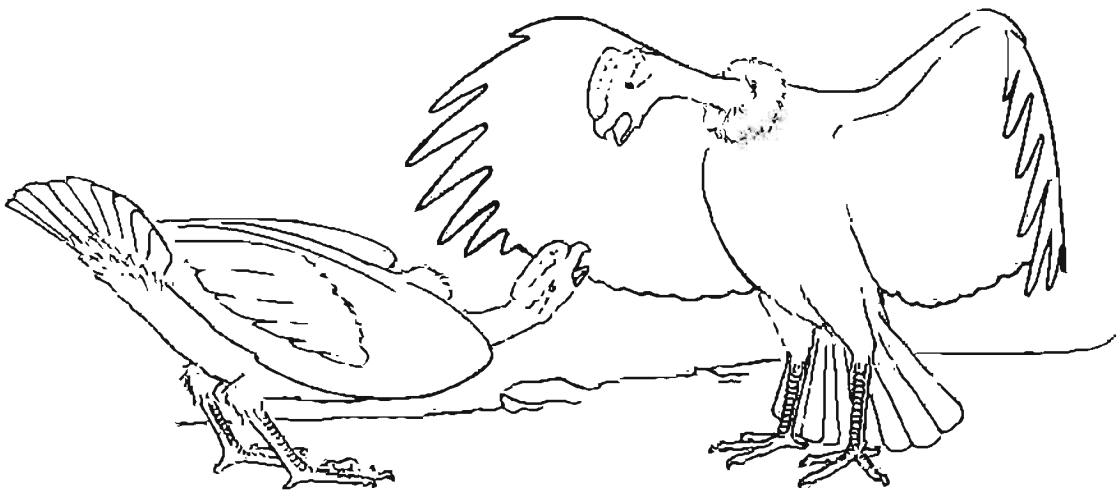


Figure 18. An aggressive encounter between two adult males at the bait. The erect male (AM1) ran at the other (AM3), stopped, pecked at the beak of the crouched bird, and then turned away.

succeeded courtship in eight of 69 bouts (12 percent, Table 13).

Pacing back and forth seemed related to courtship. Occasionally, before or after assuming a courtship posture, AF1 paced back and forth with folded wings and long axis of the body parallel with the horizon. She turned in toward the male after walking by him each time, so that her paths of movement were 8-shaped. Once she paced by the male 8 to 10 times during a 30-second period while he courted (Figure 14e); when she stopped, he mounted her.

Copulation

On 22 occasions, I observed one condor step up onto the back of another and stand there for 30 sec or more. Rhythmic motion of the abdominal region indicated attempts at coition. Both observations of female-mount-male patterns, one in Colombia and the other on Isla Zárate in Peru, are considered here as copulation postures because the sequence of motor patterns appeared no different from those observed when a male mounted a female. For all copulation patterns, I tried to monitor behavior for each stage of the sequence noting activity before and after the copulation pattern, as well.

Pre-Copulation Activities

In all of the 15 instances where activity prior to copulation was observed, the bird mounting assumed a courtship posture beforehand. In one incident, the two birds shuffled around for about 1 minute in the interval after the male courted and before he mounted. In another of these cases, each nibbled the other's head during a 7-second period after the female courted and before she mounted. In the remaining 13 instances, courtship immediately preceded copulation; in all but one of these, the bird remained in the courtship posture after mounting. One male folded his wings before stepping upon the female's back. In five observations, the female stood erect and motionless just before being mounted. In four instances, she walked or

paced beforehand. The two males that were mounted stood erect in the normal stance before the female stepped on. Both males had courted less than 1 minute before. This marked association between courtship postures and mounting by *Vultur* (1:1) contrasts with the relatively smaller fraction of one-third noted by Davis (1979) for turkey vultures (6 of 18 mountings preceded by courtship postures) and for California condors (3 of 9, combining data from Koford, 1953, p. 79; Wilbur and Borneman, 1972).

Motor Patterns

The bird mounting usually stepped on from the side or just posterior to this position near the base of the other's tail. A male on Isla Zárate attempted three times to step onto the back of a feeding female. Twice, his foot slipped off as he shifted weight to that side; on the third attempt, he mounted her. During mounting, the bottom bird usually stood motionless, with the long axis of the body forming an angle of about 30^{o} to 45^{o} with the horizontal. One female stood in a bowed position, and another sat down upon her tarsi. Once, AF1 lowered her head to the position usual in courtship just as AM1 stepped onto her back.

Head and Neck Positions

The head of the bird standing on top was usually bent downward in the courtship position and remained there until the moment of dismounting. I noted this static position in seven observations of males and in the two of females that mounted. I watched for but never detected any holding by the beak of either partner during the entire sequence. I saw one male nibble at the side of the female's head before attempting cloacal contact. Instances of head nibbling by captive condors in this stage of the copulation sequence were recorded by Whitson and Whitson (1969) and Gailey and Bolwig (1973). Davis (1979) observed it as well with wild turkey vultures. I saw one male Andean condor extend his head forward, hold it there momentarily until attempting cloacal contact, and then lay it on the back of her head. Several males raised

their heads from the courtship position to an erect stance and then lowered them again.

Head and neck position of the bird mounted varied considerably, ranging from upright, through an extended-forward position to the bowed posture characteristic of courtship. Sometimes the condor assumed several of these positions while supporting the other bird (Figure 14g-i).

Wing Position and Movement

I did not detect any motion by the folded wings of mounted condors. The position and action of the wings for the bird atop varied from motionless extension to regular flapping. In five instances, flapping seemed to help maintain balance. One male flapped a single wing once while moving the foot on that side. Two others each flapped irregularly about 10 times in apparent attempts to maintain balance while shuffling about on the female's back, perhaps during the period of cloacal contact. In three observations, males flapped rhythmically while standing on the female, one of them at a rate of 1.2 wingbeats/sec. In these instances, the period of flapping ranged from one-third to nearly the full period they stood upon the female. The axis of the downstroke motion in one case was directed forward at an angle of about 45^{o} with the horizon; in those situations where imbalance seemed to be the stimulus, the axis of motion was perpendicular to the horizon.

The wings of two males were held in positions of the courtship posture; one flexed his wings slowly but then quickly extended them again. Wings of the other moved very little, if at all. Another male held his wings open for 40, 15, and 53 second intervals, closing them twice for several seconds. He flapped them irregularly during the second and third periods. Another held his wings extended for 15 seconds, flapped them regularly for 20 to 25 seconds, and then held them half-flexed and motionless for the remaining 20 to 25 seconds that he stood on the female's back. One male, during an apparent attempt at cloacal contact, brought his extended wings down

around the female and held them there in a motionless position. Another did the same, resting the tips of his wings on the ground in an apparent effort to maintain balance (Figure 14, j,k). Captive males have been observed using wings for support during copulation (Whitson and Whitson, 1969; Gailey and Bolwig, 1973).

In the reverse copulation patterns, both of the females that mounted males flapped regularly during the entire period that they stood on the males' backs; one flapped 95 times in 69 seconds. Mounting turkey vultures held their wings out in a courtship posture or flapped them rhythmically, one at a measured rate of 2 wingbeats/min (Davis, 1979); she observed this "rowing" wing movement in 12 of 18 mountings.

Body Position and Movement

Body movements of both birds during the moments of attempted coition were often rapid, complex, and difficult to separate into distinct elements for each partner. A few positions and motor patterns were apparent, however. In about two-thirds of the copulation patterns observed, the female remained standing throughout the entire sequence. In the remaining observations, the female sat or lay. The female of a captive pair observed by Whitson and Whitson (1969) lowered her body to the ground after lifting her tail and extending and elevating her wingtips slightly. In four observations of pair 1 in Colombia, I saw the bird standing beneath the other suddenly pitch forward to a sitting or lying position, just prior, perhaps, to cloacal contact. One of these instances involved the female-mount-male pattern. In all four situations, the bird atop remained there after the pitching action, which suggests that the movement may have been part of the coition pattern rather than its termination or merely the failure of one mate to support the weight of the other.

Movements during apparent attempts at cloacal contact and sperm transfer were recorded in a few observations. A male on Isla Zárate stood atop the female in the courtship posture for

10 seconds before lowering his abdomen and rotating the tail slightly. His tail then moved rhythmically up and down four or five times across an arc of about 20 cm at the distal end at a rate of about 3 cycles/sec. This pattern occurred four times at even intervals throughout the 1-minute period that he stood upon her back. In two other observations, the measured rate of tail movement was also about 3 cycles/sec.

At the end of the copulation pattern, the bird atop usually stepped off, frequently forward over the head or neck of the other but sometimes to the side. One male closed his wings and stepped off. In two other instances, the male folded his wings after stepping off. One male stepped off to the side after the female slowly began to stand from the sitting position. Another male appeared to slip and fall to the side after attempting cloacal contact.

Durations

Durations recorded in 15 observations for the period that the male was atop the female ranged from 30 seconds to 113 seconds,with a median of 1 minute. Poulsen (1963) reported a captive male stood in a courtship posture on the back of the female for 3 minutes before copulating. I recorded four durations of 10, 15, 25 to 30, and 60 seconds for intervals between mounting and the onset of thrusting by the abdominal region. Four periods of constant thrusting were recorded at 5 to 9 seconds, 5 to 10 seconds, 8 to 10 seconds, and 20 to 25 seconds. I was unable to secure exact values because the onset and ending of the thrusting were gradual. Thrusting occurred in broken intervals throughout one 53-second period and another 1-minute period in two separate copulation patterns by AM1. Wilbur and Borneman (1972) observed an instance of copulation by California condors that lasted one-half minute and one by turkey vultures of 45 seconds. Four durations of mounting by wild turkey vultures where cloacal contact was observed ranged from 36 to 79 seconds, with a mean of 64 seconds (Davis, 1979). She reported another instance observed by J. Schmitt where three apparent copulations, about 7

seconds each, occurred during a single mounting of 35 seconds. Copulation patterns by white-backed and Rüppell's griffon vultures seen in Africa by Houston (1976) lasted 8 to 35 seconds and involved no observable courtship posture.

Post-Copulation Activities

In most of the periods following apparent copulations, I saw little evidence of interaction between mates. Usually, the male flew first within 3 minutes after he had stepped down. In six of eight intervals following copulation patterns by pair 1, AM1 flew after standing quietly for approximate periods of 3, 5, 30, 60, 90 and 120 seconds and left AF1 behind. In three of these instances, AF1 followed shortly afterward. In the others she remained behind, preening or standing quietly. After one apparent copulation, they both walked back out of sight onto another ledge; AM1 flew after 12 minutes, and she remained. In another situation, AF1 flew first about 1 minute after AM1 dismounted; he followed. When AF1 mounted AM1, he took off 15 seconds after she stepped down, and she followed immediately.

In six periods following male-mount-female patterns for other unidentified condors, the male flew first in three instances and the female in one. In 13 of 18 copulation postures observed by Davis (1979) for wild turkey vultures, the pair remained perched together for periods ranging from 3 to 75 minutes and engaged in maintenance activities, usually preening. She noted that the first turkey vulture to depart was the supposed female in 8 of 12 instances. After one apparent copulation by condors on Isla Zárate, the male returned to the carcass and fed while the female stood quietly. In a second similar instance, the female returned to feed, and the male remained behind. The female that mounted the male on the island flew first after dismounting. They nibbled at each other's head for 30 seconds before she left. Mutual nibbling also followed copulation activity by captive pairs (Whitson and Whitson, 1969; Gailey and Bolwig, 1973).

Twice I saw courtship postures follow apparent copulations, once by both mates and once

by only the male that had mounted. Davis (1979) once saw the male turkey vulture that had been mounted assume a courtship posture after copulation. In these instances, sperm transfer might not have occurred in the copulation posture.

Coition With Sex Roles Reversed?

The close similarity in the complete patterns of male-mount-female and female-mount-male postures suggest that both positions may function in the transfer of sperm. In the female-mount-male observation on Isla Zárate, I saw the abdominal region of the female thrusting rhythmically as the male shuffled about several steps. One bird was atop the other for approximately 1 minute with the pair on Isla Zárate and 69 seconds with pair 1, values similar to those for male-mount-female observations (see p. 89-90). The pitching action of the bottom bird and the motor patterns before and after by pair 1 resembled those of male-mount-female positions. Although Gailey and Bolwig (1973) recorded female-mount-male patterns for captive pairs, they did not report any attempts at cloacal contact.

Frequency Comparison With *Gymnogyps*

Andean condors may participate in sexual activity, copulation patterns in particular, more often than California condors. Koford (1953, pp. 77,79) reported observing sexual display by *Gymnogyps* on more than 30 occasions, with a possible copulation on only one. In contrast, I recorded 22 copulation patterns by *Vultur*, with a frequency of courtship observations about two to three times the number Koford recorded for *Gymnogyps*. Although these values serve only as rough indices, they suggest that the ratio of frequencies for copulation to courtship are higher with *Vultur*. With turkey vultures, courtship seems a relatively rare behavior; Davis (1979) saw no courtship postures by turkey vultures except prior to mounting.

Mate Relations of Individual Pairs

Associations

A comparative study of mat associations and activities of two adult pairs, a nesting and a non-nesting pair, was conducted by monitoring the movements and activities of both pairs simultaneously. The roost areas of each pair were visible from one point. In one measure of the comparison, I calculated the amount of time mates spent alone and in each other's company and examined how these fractions varied for each pair according to general activity and period of the day (Table 16). Data from another nesting pair, pair A, were also considered even though they were recorded at a different location and time. The presence of additional variables must bias those comparisons with pair A but a few relationships seem strong enough to warrant noting. The activities of pair A were observed a year after those of pairs 1 and 2 and in the same general area, so it is possible that either one or both mates were the same adults observed before. For simplicity, they will be treated here as another pair.

I examined the proportion of time that members of each pair spent alone or together in the observation area. All six condors frequented the roost area more often when accompanied by a mate than when solitary. Mates of a non-nesting pair, pair 1, seemed more closely associated than the mates of the nesting pairs; more than two-thirds of the time one member was observed, the other was present as well, whereas a similar fraction for time observed together was only about one-half with both nesting pairs (Figure 19). During the pre-foraging part of the day, mates of pair 1 appeared to perch near each other (< 10 m) more often and for longer periods than mates of the nesting pair 2 (Table 16), another measure, perhaps, of a difference in mate attraction. Although differences were not statistically reliable, members of the non-nesting pair were also observed to roost separately at night less often than the nesting pairs (Table 17). In only 1 of 9 instances did a non-nesting mate roost alone, whereas nesting mates roosted alone in 8 of 24 observations (Figure 19).

Table 16. Mate associations and activities at the roost area. A tally of durations for different contexts observed from 11 November 1968 to 2 March 1969 for pairs 1 and 2 and from 9 March 1970 to 29 April 1970 for pair A. The roost area for pairs 1 and 2 was observed for 399 hours over 45 days and the roost area for pair A for 145 hours over 20 days. In parentheses are the number of sample days when durations were recorded for that context.

		Percent of total time observed in various contexts					
			Pair together				
	Total min one or both mates observed	Flying	<400m, >10m apart	<10m apart	Male perched Female flying	Female perched Male flying	Total[a]
Pair 1: Pre-forage time	1830(22)	1.5(11)	6.7(10)	15.8(14)	0.2(3)	0.3(2)	24.6(18)
Remainder of day	4273(34)	10.3(26)	9.9(19)	18.5(22)	1.1(14)	4.2(23)	43.9(26)
Pair 2: Pre-forage time	3079(21)	0.5(5)	9.2(9)	7.0(9)	0.6(5)	0.1(2)	17.4(10)
Remainder of day	6393(30)	6.4(19)	7.5(19)	18.3(17)	1.4(15)	0.9(11)	34.5(24)
Pair 2: Pre-forage time	1498(12)	0.2(1)	11.0(5)	9.1(5)	0.0(1)	0.3(2)	20.7(7)
Remainder of day	1532(17)	5.7(7)	3.8(4)	20.5(8)	0.3(2)	1.2(5)	31.5(11)

	Percent of total time observed in various contexts					
	Male alone			Female alone		
	Flying	Perched	Total	Flying	Perched	Total[a]
Pair 1: Pre-forage time	0.1(2)	3.0(4)	3.1(5)	0.3(3)	2.0(3)	2.3(3)
Remainder of day	1.7(10)	8.6(12)	10.3(16)	2.0(9)	13.7(14)	15.8(14)
Pair 2: Pre-forage time	0.8(7)	10.3(8)	11.1(8)	0.3(4)	3.7(6)	4.0(6)
Remainder of day	1.7(19)	17.9(22)	19.6(22)	1.6(12)	11.8(12)	13.5(15)
Pair A: Pre-forage time	0.6(3)	21.3(5)	22.0)5)	0.5(3)	6.2(5)	6.7(5)
Remainder of day	4.3(8)	11.6(9)	15.9(10)	0.3(4)	2.9(3)	3.2(4)

[a] Due to the rounding error percent totals may not exactly equal row sums.

Nesting adults frequented the nest and roost area more than the non-nesting adults. Mates of pair 1 were observed in their roost area an average 15 condor minutes per hour of observation. Pairs 2 and A, both caring for feathered nestlings in their roost areas, visted the area an average of 24 and 21 condor minutes per observation hour. Males of both nesting pairs frequented the nest-roost area alone more than their mates did alone during period both before and after the onset of foraging. A sexual difference in the degree of nest attention seems inadequate for explaining the relationship; although AM2 did attend to the nestling more than the female, the male of pair A did not. A pair of breeding turkey vultures observed by Davis (1979) perched together in the nesting area relatively more often than the three pairs of condors that I observed. Of the time both turkey vultures were observed present in the nest area, they perched together 46.5 percent of the time. For the condor pairs representative values for the time perched within 10 m of one another ranged from 7.0 to 18.5 percent (Table 16).

Activities

Mates may stimulate each other to fly from their perch. When one mate flew the other was likely to follow, often within 15 seconds. The number of observations for flight by AM1 while AF1 was perched exceeded that of the nesting pairs (Table 18). This trend was also apparent in an analysis of lead-follow relationships described in the next chapter; for pair 2, the male usually followed take off by the female while the reverse was true for pair 1. These flights by AM1 may have represented some part of a courtship sequence stimulated by the presence of AF1. A comparison of flight frequency for lone condors with those accompanied by a mate may provide another measure of social stimulation. All of the six adults flew from one-twelfth to one-eighth of the time that they were observed alone in the roost area (Table 18). United mates of pairs 2 and A flew simultaneously for similar proportions of time, whereas mates of pair 1 flew even more often when together than when alone. All these proportions of time flying

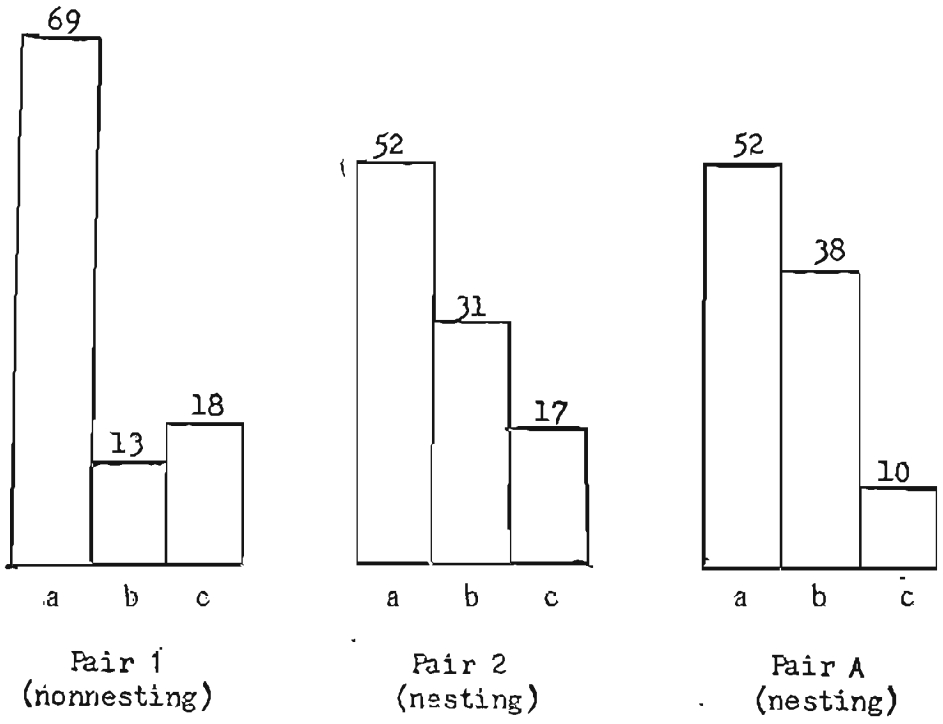


Figure 19. Percent of time one or both mates observed at the roost area (a) together, (b) male only, or (c) female only. Data from Table 16.

Table 17. Roost attendence at night by mated pairs. To prevent errors introduced by undetected late arrivals or early departures, only those data recorded on overnight trips to the roost area are included.

	Percent observations				Total no. observations
	Both members	Male only	Female only	Neither	
Pair 1 - nonnesting	80	10	0	10	10
Pair 2 - nesting	60	30	10	0	10
Pair A - nesting	71	21	7	0	14

together are larger than expected; in random systems, the expected value for time spent flying by each pair is the product of the fraction of time spent flying alone by each mate. These relationships for the three pairs suggest that mates stimulated each other to fly, although it is possible that mates may have reacted independently to the same factors. Some flights, for example, may have served to cool the birds; flying together would then occur more often than expected if it was warmer when mates were together.

The non-nesting pair (1) was sexually active more often than either of the nesting pairs. I compared the frequency of courtship and copulation postures observed for pairs 1 and 2 with expected values derived using appropriate measures of observation time for each pair page number (see p 82- 83 for description of the technique and Table 19 for frequency and observation time values); differences between pairs were significant both for courting[9] and copulating.[10] Courtship bouts by the nesting pair occurred at a mean rate of 9.3 per 10 hours of observation time, whereas these values were 2.8 and 0.4 for the nesting pairs 2 and A, respectively. Copulation postures by pair 1 occurred at a mean rate of three per 10 hours of condor observation; none was seen for the nesting pairs. The variations are more likely due to differences in reproductive status rather than to individual characteristics. As noted earlier, courtship by nesting *Gymnogyps* was also rare (Koford, 1953, p. 78).

Mate relations of the two pairs differed not only in the frequency of sexual activity like courtship and copulation but in the patterns of a few other interactions as well. One peculiar posture of tilting forward (Figure 14k) occurred often in the relations at the nesting pair 2. I saw it six times and only once with pair 1. Recorded durations of the tilted posture ranged from 4 to about 30 seconds. Both mates of pair 2 tilted forward in those postures during three protracted nibbling interactions. In 11 other nibbling bouts, the long axes of their bodies remained horizontal. This tilting did not occur in any of the protracted nibbling interactions observed for

Table 18. Time spent flying in the roost area in different settings. This table assembled with the same raw data used to construct Table 16[a].

	Percent time flying when:			
	Mates are together[b]			
	Both aloft	One aloft	Male alone	Female alone
Nonnesting pair 1	17.2	8.5	13.5	13
Nesting pair 2	13.3	5.7	8.3	11.3
Nesting pair A	11.3	3.7	13.0	8.3

[a] Values represent the percent of time aloft considering each of the three contexts separately, whereas in Table 16 values for all contexts represent percentages of the total time birds were observed.

[b] Mates < 400m apart

pair 1.

NESTING

The Nest

Nest sites of the Andean condor are difficult to locate. No nest structure is obvious. Caves used are usually one of many that riddle long, inaccessible canyons. Adults may visit the nests infrequently, and then they are often visible at the cave entrance for only a moment. I observed only two occupied nests during the field study and each contained a chick 5-6 months of age. I was unable to obtain any information on egg laying or incubation by wild Andean condors.

The nest of pair 2 was located 50 m below the rim of a 650 m canyon wall directly above the confluence of the Rio Pasto and Rio Juanambu. Nest elevation was 1300 m above the sea. About 120 cm high and 60 cm in width, the cave entrance led to a hole that extended back into the rock at least 2 m, where it descended and hooked to the right. A soil-covered ledge about 60 cm wide and 150 cm long lay in front of the entrance. During the observation period from November 1968 to March 1969 the entrance with its northeast exposure was never touched by direct rays of the sun.

The nest cave of pair A faced east and was exposed to sunlight during the morning. I observed this nest from March to May 1970. The nest was located at a similar elevation and on the same side of the Rio Pasto canyon, 2 km upstream from the nest of pair 2. The cave looked out about 200 m above the river and 300 m below the canyon rim. A narrow ledge in front descended away from a cave entrance that was about 1.5 m high and half as wide (Plate 20). I visited another nest site 10 km upstream on the Rio Pasto that had been occupied a decade earlier (according to local farmers). This location was on the east side of the canyon, about 30 m below

Table 19. Frequency of courtship and copulation postures recorded for mated pairs in Colombia.

	AM1	AF1	Pair 1	AM2	AF2	Pair 2	Male A	Female A	Pair A
No. hr mates observed apart[a] ≤400m and >10m									
male perched (A_1)	48.2			69.2			22.6		
female perched (A_2)		51.4			68.0			23.2	
either mate perched (A_3)			52.7			71.0			23.4
<10m both perched (B)			30.0			39.9			15.0
No. days courtship observed	11	12	14	10	1	10	0	1	1
No. courtship bouts observed	22	21	49[b]	19	1	20	0	1	1
No. courtship bouts per 10 hr observation time (A/10)	4.6	4.1	9.3	2.7	0.1	2.8	0	0.4	0.4
No. days copulation postures observed			8			0			0
No. copulation postures observed			9			0			0
No. copulation postures per 10 hr observation time (B/10)			3.0			0			0

[a]Occasionally perched condors were not visible but their locations were still known. For this reason, some values for observation time given in this table are less than those presented in Table 18 where relative positions and not activities are compared.

[b]Sex of courting mate in pair 1 unknown in six observations.

the rim at an elevation 1500 m above the sea. Both the cave entrance and the ledge were about twice as large as those described above, and the epiphytic vegetation growing around it was more lush. A small cave about the size of those described for pairs 2 and A was the site of a nest near La Paz, Ecuador, that had been occupied in 1963. The cave was located approximately halfway down a series of escarpments 200 m high. Exposure was northerly. Mammalian carnivores had access to none of these nests. In desert habitats of north-central Chile, William Mille (pers. comm.) of Vallenar visited two condor nest caves, one containing an egg and another a chick. Both caves could be approached and entered on foot. The cave entrance to one was large enough for him to stand in upright; caves used by California condors for nests vary in size to similar extremes (Koford, 1953, pp. 81-82). The egg Millie found lay in a sandy depression near the end of the smaller cave.

Even though the nests observed in Colombia and Ecuador were less accessible to humans, they fit among numerous ledges and rock outcroppings that would have served well as frequent perches for the short flights of young and inexperienced birds. I found no evidence of caves nesting on the many large and comparatively smooth-faced cliffs along the canyons.

Although pair 1 never incubated an egg during the 4-month period of observation, they did regularly frequent one cave in the center of their roosting area, a cave slightly smaller than the nest cave of pair 2. I saw both adults disappear into the cave together on four occasions for durations ranging from 6.5 to 15 minutes. I saw one member of the pair, usually the female, enter the cave alone on 11 occasions and remain inside, hidden from view, for periods ranging from 2 minutes to 5 hours. Although this pair courted and copulated often during this time, no regular use of the cave followed; gradually the pair began to frequent the area less often.

Egg Laying and Incubation in Captivity

Plate 20. The nest cave of pair A in Colombia. The cave is in the lower center (see arrow). Note the adult just leaving the nest.

Andean condors have bred and raised young in a number of captive conditions. A few zoos in Europe and the United States have reported reproductive success by caged Andean condors (Apolinar, 1914; Janda, 1938; Lint, 1960; Dekker, 1967; Klös, 1953; Faust, pers. comm.). Eight young have been reared in captivity at the Patuxent Wildlife Research Center and five at the Bronx Zoo. Lint (1960) followed the stages of egg-laying, incubation, and nestling growth for nine Andean condors raised at the San Diego Zoo. He reported that both parents incubated a single white egg, approximately 200 g in weight and 10 cm in length. If the egg was accidentally destroyed, a second was laid. He recorded an incubation period of 56 days for each of nine eggs. Greyish-white down, about 5 cm in length, covered young chicks. Newly-hatched males bore a tiny crest on their heads. First flight did not occur until about six months after hatching, when the fully feathered chick weighted about 11.25 kg. In the West Berlin Zoo, Klös (1973) reported that the male *Vultur* regularly incubated from 0900 to 1700 hours and the female for the remainder of the period. He reported four incubation periods of 50 days and two of 60 days. In four other species of New World vulture, the turkey vulture, the California condor, the king and black vulture, where incubation of wild birds has been observed, both mates incubated (Coles, 1938,p. 297; Koford, 1953, p. 87; Smith, 1970; Steward, 1974).

PARENT-YOUNG RELATIONS

Feeding

When the adult landed at the nest, feeding by regurgitation usually followed directly. In 11 of 21 observations, it occurred immediately after the parent alighted. If the adult paused before feeding, it usually did so by standing quietly on the ledge for 10 to 15 seconds. In one exception, AM2 landed at the nest, entered the cave, and sat on his tarsi for 10 minutes, facing

and preening feathers on the back of the chick. He also preened himself intermittently. Then he fed the chick in a 1-minute bout.

The nestling may be able to determine the adult's readiness to feed. The chick did not beg until the end of the 10-minute period described above, just before he was fed. Possibly, the adult does not begin feeding until the chick demonstrates a readiness to take food. In one instance, however, AM2 appeared to seek the nestling. On this occasion, the begging chick was less animated than usual. After AM2 landed, the chick faced the cliff with his head behind a rock on the ledge. The parent walked around the rock and approached the nestling before feeding him. Usually the begging chick approached the adult, often following him about on the ledge or in and out of the cave between feeding bouts. Pairs 2 and A fed their nestling on the ledge, in the cave, or at the cave entrance. Multiple feeding bouts of a single visit sometimes occurred in all of these locations.

Motor Patterns of Feeding

In the feeding bout, the adult tilted forward until the long axis of the body was within a zone 30^{o} above and below horizontal. The neck extended forward so that the head, tilted slightly to one side, was from 5 to 25 cm above the ground with the beak pointing downward, usually at an angle of 45^{o} with the horizon. The chick inserted his beak up to his nostrils into the adult's beak on the side tilted up. A pumping-like action by the neck and body of the adult followed. In each of three observations that included both parents of pair 2, heads of chick and adult moved back and forth at a measured rate of 2 cycles per second. Koford (1953, p. 99) measured the same rate of movement for *Gymnogyps*. Apparent motions of regurgitation produced undulating movements of the adult neck and a rocking fore and aft of the body, all in rhythm with head movement. Feeding ceased when the adult withdrew head and neck and resumed a normal stance. Although the parent normally remained standing during the feeding session, the crus and

tarsi were flexed enough, so that the tarsi of the crouched bird formed angles with the ground as low as 45°. Sometimes adult and chick turned about while feeding. In one 100-second feeding bout, AF2 backed up continuously, turning almost one full circle on the ledge in front of the cave. Motor patterns in the parental feeding bouts of *Vultur* and *Gymnogyps* seem to differ little if at all (Koford, 1953, pp. 99-100). In a fascinating account of observations made no more than 3 m from wild nesting black vultures, Stewart (1974) noted that the adult usually initiated feeding by extending an open bill toward the nestling.

Amount of Food Delivered

The volume of food given to the condor chick appeared to vary considerably among feedings. On three occasions, I noted parents with crops apparently still full after feeding the chick. Once, AM2 flew from the nest with a crop that seemed only slightly less full than when he arrived. On another occasion, the chick displayed a full crop after being fed three times. Once, AF2 arrived at the nest with a full crop, fed the chick, and returned 27 minutes later to feed him again, leaving this time with a crop less than half full. The chick apparently received 400 g or more of food from these two visits (Table 42). I was unable to determine if feeding durations were proportional to the amount fed.

Feeding the Volant Juvenile

Although I saw few relations between parent condors and the volant juvenile, I did see on three occasions an adult feed a volant juvenile near La Paz, Ecuador. In one bout, a young condor shuffled a full circle around the adult during the feeding. Once, they fell from the perch; their heads remained in contact for a moment after they were airborne. Then, they both circled and gradually flew from view. In Colombia, young birds of both pairs 2 and A were observed for one week each on perches several meters above their nest caves. These new perches could be reached only by circling out into the canyon, gaining altitude, and alighting above. Behavior of

the juvenile and relations the parents in this early part of the volant stage seemed no different from that of the nestling period.

Durations and Activities of the Nest Visit

The extent and frequency of separate feeding bouts were difficult to obtain because of shadows and extraneous motion. In a few clear observations I noted that AM2 usually fed the chick more than once before taking off ,whereas his mate tended to engage in only one feeding bout. On six separate visits by AM2, I saw three or more separate feeding bouts each time, some enduring for 10 to 15 seconds, others up to 70 or 80 seconds. On two visits by AM2, motions of feeding continued without interruption for 4 minutes. Once, I saw AF2 feed the chick continuously for 80 seconds.

Usually most parents remained at the nest for 3 to 8 minutes, which was three or four times longer than the feeding period (Table 20). Sometimes they nibbled at or preened the chick. Otherwise, they sat or lay quietly on the ledge or in the cave, engaged in various maintenance activities like preening, rousing, side and bow stretching, defecating, sunning, or head and neck wiping. Wiping was a common activity following feeding although occasionally it occurred between feeding bouts. Sometimes, AF2 paced about on the ledge or in and out of the cave. Once she walked in and out of the cave eight times. The longest durations recorded for a nest visit were 236, 147, and 98 minutes, all by AM2. The maximum period recorded for AF2 was 90 minutes.

Adults sometimes seemed to avoid extended nest visits. Three times, I saw the adult male visit and feed the chick in the nest cave, while it was raining; each time, the male flew out into the rain and landed on another perch nearby. Perhaps adults avoid prolonged contact with the youthful activity of older nestlings. I never saw an adult roost at the nest. In contrast to *Vultur*, however, *Gymnogyps* parents appear to spend much less time at the nest; for one pair,

Koford (1953, p. 100) recorded 6 minutes as the longest stay after feeding. Durations recorded for the turkey vulture have also been shorter; Davis (1979) reported a mean duration of 95 seconds (n=9) for nest visits and 34 seconds (n=11) for feeding time.

Nest visits by AF2 were relatively brief (Table 20); about half of those recorded were 3 minutes or less. Durations at the nest were significantly longer by AM2[11] and by both members of pair A,[12] averaging around 7 to 8 minutes. Differences in durations were not significant for the male and female of pair A,[13] nor were they between this pair and AM2.[14] AM2 also seemed to feed the chick longer than AF2. The median duration recorded for AM2 was 117 seconds compared to 65 seconds for AF2. I did not test for differences between durations of the feeding bouts because of possible biases due to problems in viewing. Shorter feeding durations by one parent might reflect a tendency to feed in the cave out of view. Another source suggests, however, that total feeding time by AF2 was less than that of AM2. On four occasions, AF2 visited the nest without feeding the chick at all; this was never seen for AM2 nor for either member of pair A.

In general, curves obtained by plotting logarithms for the cumulative frequency of durations at the nest against interval durations were slightly concave in shape, indicating that more short intervals were recorded than expected (Figure 20, see also p. 80). Distributions of this type suggest that the probability the parent would take off immediately declined the longer they stayed at the nest. Such a relationship might reflect activity levels of the chick; perhaps the adults remained in attendance when the nestling was quiet (Figure 20).

Frequency of Nest Visits

The frequency of nest visits by parent condors also varied according to the individual. I saw AM2 land at the nest more than twice as often as AF2; no sexual difference was recorded for pair A (Table 20). Individual differences or seasonal and temporal changes in behavior may

Table 20. Durations of parental nest visits and feeding bouts with the chick.

	AM2	AF2	Male A	Female A
Nest visit				
No. observations	56	25	13	13
Duration (sec.)				
Median	475	183	445	402
First decile	120	68	124	37
Ninth decile	3142	1400	2297	5220
Feeding				
No. observations	27	16	2	2
Duration (sec.)				
Median	117	65	105	58
First decile	51	6	-	-
Ninth decile	191	144	-	-

account for the variation. Priority of access to food by the dominant class of adult males might affect the frequency of nest visits if the dominant males were able to feed the chick more often. Sex of the chick could also be related to a difference in parental attentiveness. Father-son or mother-daughter bonds might be advantageous for the juvenile in early social orientation, particularly in learning patterns of social behavior useful to one sex.

The daily frequency of nest visits and feeding bouts by each adult probably depends on many factors, one of which may be the availability of food. I recorded the largest number of nest visits for one day, five by AM2 and two by AF2, when the pair fed on a steer that had fallen into the canyon less than 400 m from the nest. On two other days when foraging condors were away from the nest and roost area for long periods, the nest was visited only once, each time by AM2. For 27 days of observation, the mean number of nest visits by both parents in one day was three. For the turkey vulture, Coles (1938, p. 327) reported feeding did not occur more than twice a day; Davis (1979) recorded 25 instances of feeding for 107 hours of observation, a mean of 2.3 feedings per day. A pair of closely monitored black vultures were found to engage in 15 to 20 feedings in the daylight with some probable feeding at night during the brooding phase; in subsequent phases, the young were usually fed in only three or four sessions per day (Stewart, 1974). Koford (1953, p. 97) recorded a usual feeding rate of twice a day for *Gymnogyps*. These differences may represent variations in food availability and the phases of nesting.

Feeding frequency by one parent might also depend on the activity of the mate. Once AM2 appeared gliding over the canyon rim about 1 minute after AF2 had landed at the nest. She flew then without feeding the chick. AM2 landed at the nest and fed the nestling. She may have been prepared to feed the chick until her mate appeared. He might have fed more recently. The female visited the nest five times one day and four another when the male failed to visit it once. To see if the number of visits by one parent depended on the number of visits by the other, I

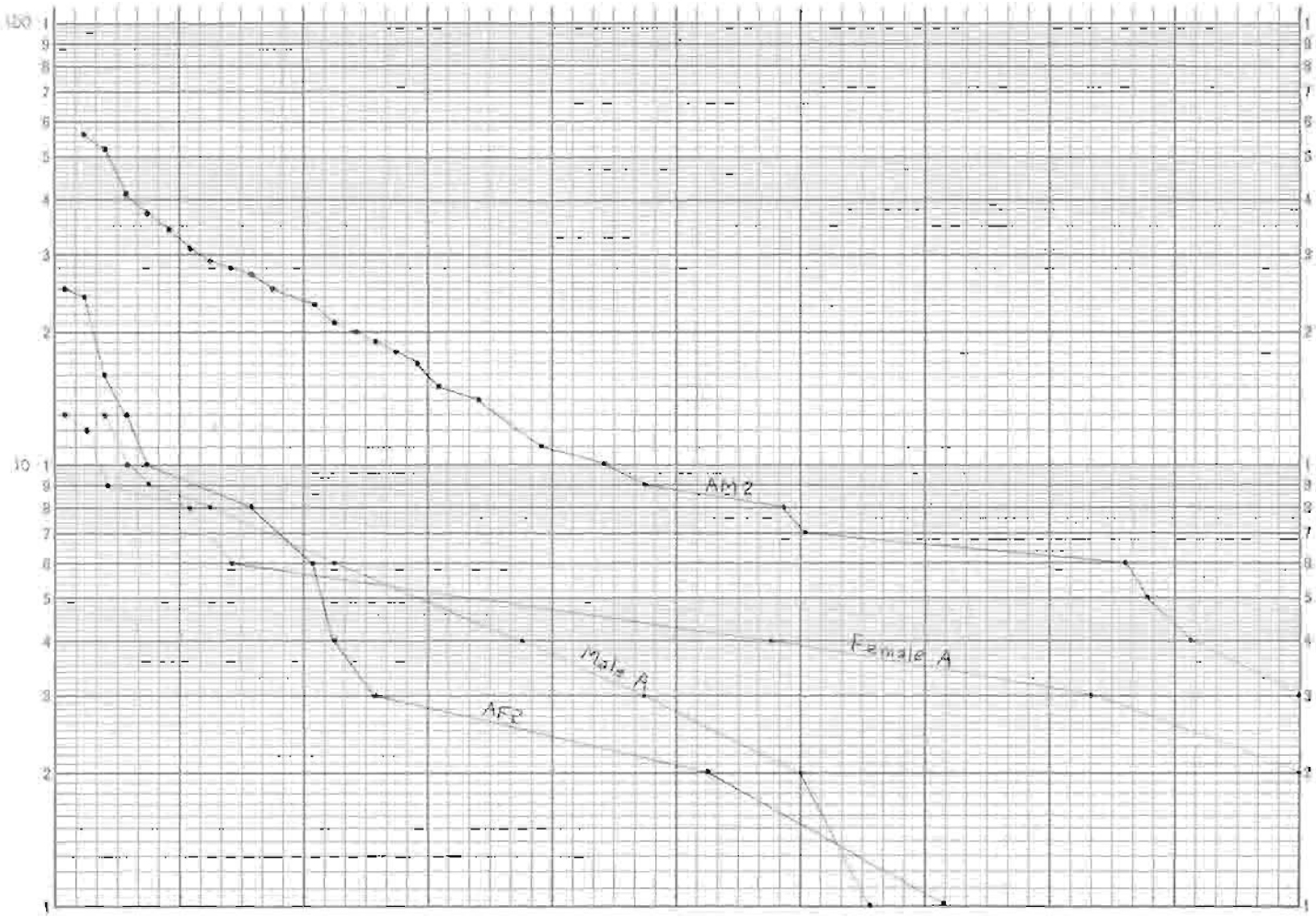


Figure 20. Logarithms for the cumulative frequency of durations at the nest plotted against interval duration. Separate curves drawn for each parent (AMA, n=13; AFA, n=13; AF2, n=25; AM2, n=56). The five longest durations were not plotted on this graph (AM2 98, 147, and 286 min; AFA 90 and 60 min).

tested for but found no significant relationship, either direct or inverse, in the number of daily nest visits between parents (Table 21). Mate relationships in feeding the young may well be too complex to detect with this kind of analysis and sample size. Feeding timetables for the young probably reflect a complex set of responses by two foraging parents, not only to food and the chick, but to the feeding capability of each other as well.

Nest visits by *Gymnogyps* were less frequent that those of *Vultur*. Kofor (1953, p. 97) noted that the "same adult was not seen to enter nest 1 twice a day." He also recorded a few days when nestlings were not fed, once even when the parents were apparently unaware of any human presence. I recorded only one day when the chick went without a feeding and this occurred during the week following a major disturbance; I had climbed down to the nest to weigh and measure the chick.

Time of Day of Feeding

I found no evidence of preferred hours of daylight for visiting the nest and feeding the chick (Table 22). The frequency of nest visits distributed according to the time of day did not vary significantly within or between pairs nor did combined totals with expected values calculated using the proportion of observation time for each hour.[16] The lack of evidence for preferred feeding hours indicates that feeding occurred at a fairly consistent frequency over the daylight periods, even before foraging occurred.

The earliest and latest feeding times recorded were 0621 and 1758 (+5 GMAT) compared to 0855 and 1800 (+8 GMAT) recorded by Koford (1953, p. 97) for *Gymnogyps*. Earliest feeding times for *Vultur* occurred just after sunrise while those of *Gymnogyps* occurred about 3 hours after sunrise; late feeding times for both species were recorded in the late afternoon or evening. According to Koford (p. 96), most feeding visits by the California condor parents happened between 1000 and 1700. The roosts and nests of *Gymnogyps* were not often in the

Table 21. Number of nest visits recorded per day by members of pair 2.

		No. visits per day by AM2					
		0	1	2	3	4	5
No. visits per day by AF2	0	0	5	5	4	0	1
	1	0	2	3	0	0	0
	2	0	1	1	0	0	2
	3	0	0	0	1	0	0
	4	1	0	0	0	0	0
	5	1	0	0	0	0	0

same area, which may explain why earlier hours of daylight were not used to the same degree as they were by *Vultur*. Possibly, the birds watched by Koford did not visit the nest before foraging. Turkey vultures observed by Davis (1979) in Texas fed their nestlings most often in late morning, 0900 to 1100 (+6 GMAT) specifically.

Other Relations

Other than feeding, the most apparent activity observed in relations between adults and young was social preening. The patterns seemed to be unidirectional. Adults regularly preened their young but I never saw a nestling or juvenile preen feathers of his parent. Adults usually sat on their tarsi while preening the nestling, but occasionally they stood. Young condors sat, lay, or stood while being preened. Durations recorded for these preening bouts ranged from a few seconds to over half an hour. The back and wings were preened most often. Usually, the chick made no obvious response.

Mutual head nibbling occurred frequently but bouts were brief, usually less that a minute. Once, however, the female of pair A sat down on her tarsi, facing the chick on the ledge, and the two engaged in a bout of head play that lasted for almost 15 minutes. Then, 40 minutes later, the chick nibbled at the adult's head while she sunned. Assuming that the *Gymnogyps* pairs observed by Koford and myself were representative, nibbling and preening relations between parents and nestling *Gymnogyps* must be less pronounced than those of *Vultur* since they spend much less time at the nest. Such long bouts of nibbling or preening by *Vultur* might be characteristic of mother-daughter of father-son relationships (see p. 103). I did not see the male of pair A ever engage in a protracted nibbling bout with the female chick. AF2 preened the male nestling, but I never saw any bouts as long as those observed with AM2.

Table 22. Feeding visits to the nestling and the time of day. Data from Colombia for 42 days of observation from 22 November 1968 to 4 January 1969 and 15 April 1970 to 16 May 1970.

	Time of Day												
	0500-0659	0700-0759	0800-0859	0900-0959	1000-1059	1100-1159	1200-1259	1300-1359	1400-1459	1500-1559	1600-1659	1700-1759	Total
No. and percent (in parentheses) feeding visits observed													
Pair 2: AM2	0(0)	4(7)	2(4)	10(18)	4(7)	6(11)	5(9)	7(12)	4(7)	8(14)	6(11)	0(0)	56
AF2	1(4)	0(0)	4(16)	3(12)	0(0)	5(20)	2(8)	2(8)	2(8)	2(8)	4(16)	0(0)	25
Identify unknown	0(0)	0(0)	1(33)	0(0)	0(0)	0(0)	1(33)	0(0)	0(0)	1(33)	0(0)	0(0)	3
Pair A: Male	0(0)	1(8)	0(0)	1(8)	1(8)	1(8)	0(0)	1(8)	0(0)	3(23)	4(31)	1(8)	13
Female	1(8)	1(8)	5(38)	0(0)	1(8)	1(8)	1(8)	2(15)	0(0)	1(8)	0(0)	0(0)	13
No. observation min													
Pair 2	663	819	1495	1560	1530	1500	1500	1500	1500	1589	1493	917	16,066
Pair A	324	780	780	735	720	720	720	720	720	720	765	727	8,431

BEHAVIOR OF THE YOUNG

Positions and Stances

The nestling condor of pair 2 spent fewer daylight hours inside the cave than the young of Pair A (Table 23). Both nestlings were the same age, about 5 to 6 months old, but nestling 2 spent only about one-third of the daylight hours in the cave compared to a value of two-thirds for nestling A. The difference can probably be attributed to the variation in topography around the nest cave. A wide and level ledge lay in front of the nest cave of pair 2, whereas the cave entrance use by pair A opened onto a narrow rocky ledge that descended to the edge of the cliff face. The area outside the cave afforded nestling A comparatively little space to move safely and few, if any, locations suitable for sitting and lying.

When nestling A was visible outside of the cave, I saw her only in standing positions, whereas nestling 2 often sat or lay, usually during 30 to 40 percent of the observation time (Table 23). These rest positions were used less often by nestling 2 in the morning from 0800 to 1000. The median duration recorded for 69 periods of standing quietly in one place by nestling 2 was 15 minutes (first decil, 2; ninth 122) 66 periods of sitting or lying, it was 22 minutes (first decile, 5; ninth, 84). Movement in and out of the cave and flapping or leaping often separated periods of inactivity in these different positions.

Nestling 2 spent more time inside the cave during morning and evening hours; I found no similar trend for nestling A but sampling periods were fewer (Table 23). Data on the proportion of time spent by the nestlings in various stances and different locations were gathered and analyzed for five consecutive periods of observation ranging in extent from 5 to 12 days. No consistent trends or patterns were obvious from period to period.

Flapping and Leaping

The feathered nestlings were active in bouts of leaping and flapping, usually two or three

Table 23. Observed time spent inside the cave and in sitting or lying positions by nestlings 2 and A at different hours of day. Data gathered during 20 full days of observation from 22 November 1968 to 23 December 1968 and during 10 full days of observation from 15 April 1969 to 29 April 1969.

	Time of Day											
	1600-0659	0700-0759	0800-0859	0900-0959	1000-1059	1100-1159	1200-1259	1300-1359	1400-1459	1500-1559	1600-1659	1700-1759
Hrs observation time												
Nestling 2	9	10	20	20	20	20	20	20	20	19	17	8
Nestling A	2	10	10	10	10	10	10	10	10	10	9	6
Percent observation time in the cave												
Nestling 2	73	53	38	28	18	24	26	21	21	27	30	56
Nestling A	79	78	59	83	72	70	66	76	78	62	45	51
Observation time that nestling stance was visible (min)												
Nestling 2	119	192	494	514	561	836	651	681	780	756	593	189
Nestling A	30	146	215	88	176	206	212	155	163	232	309	215
Percent observation time in sitting or lying positions												
Nestling 2	38	38	16	10	32	43	43	32	34	28	32	25
Nestling A	0	0	0	0	0	0	0	0	0	0	0	0

times a day. Nestling 2 frequently faced the cliff and leaped back and forth on the ledge flapping his wings. Both legs were extended, and his neck stretched upward. Individual leaps to the side ranged from 60 cm to 1 m.

Bouts of walking or turning from side to side with outstretched motionless wings often interspersed periods of flapping. Following protracted bouts of flapping, his wings sometimes hung down limply, with the wrists 10 to 20 cm below their usual position.

The restriction of level space around the nest limited movements of nestling A. She usually stood sideways in the cave entrance when flapping. Her wingtips frequently struck the rock when she turned from side to side. Sometimes she stopped moving the wing striking the rock, while she continued flapping the other. Many wingbeats were of reduced amplitude; wingtips often moved through arcs only 30 to 45 cm. The frequency of these smaller wingbeats were usually three cycles per second compared to two per second for those of nestling 2.

Durations recorded for 18 periods of leaping and flapping activity by both nestlings ranged from 6 seconds to 30 minutes, with a median of 90 seconds. Short pauses frequently interrupted the extended periods of activity. The number of wingbeats for 54 bouts of continuous flapping ranged from two to 25, with a median of five. Koford (1953, p. 114) reported 15 wingbeats as the maximum observed for a perched juvenile *Gymnogyps*; the usual number was five. Turkey vulture nestlings may also exercise for comparatively shorter durations; four bouts of flapping and leaping timed by Davis (1979) ranged from only 3 to 22 seconds.

Flapping and leaping by both nestlings occurred more often than expected from 0900 to 1200 in the morning and after 1800 in the evening and less often than expected from 1400 to 1800 in the afternoon (Figure 21). Expected values were calculated by multiplying the proportion of observation time for each hour times the total number of flapping or leaping bouts

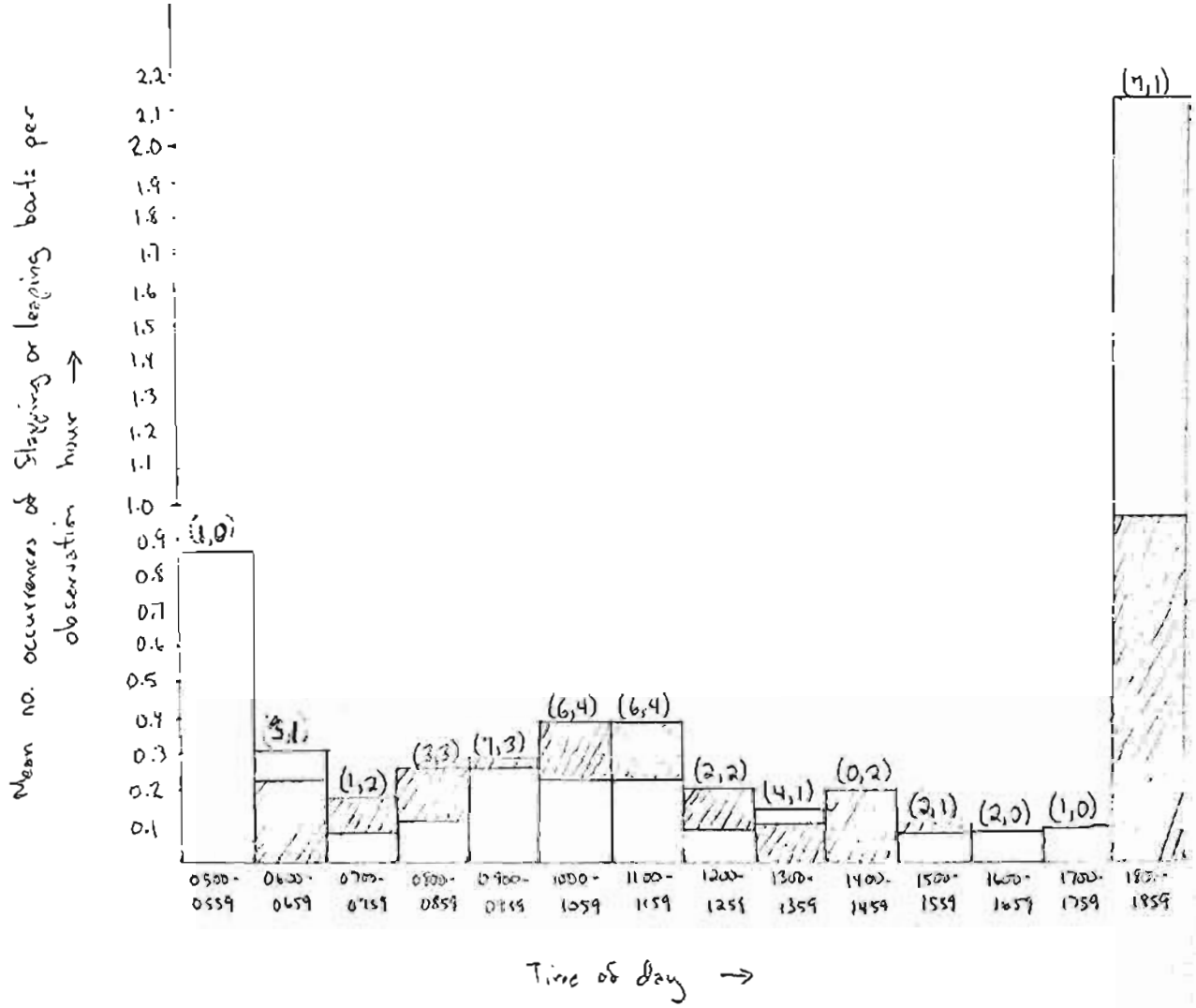


Figure 21. Flapping and leaping activity at different times of day by nestling 2 (open bars) and nestling A (cross-hatched bars). Number of bouts observed in parentheses (nestling 2, first value; nestling A, the second).

observed for both nestlings. Differences between expected and observed values were significant.[19] Bouts of flapping or leaping occurred at an average rate of 0.16 occurrences per hour of observation for nestling 2 and 0.21 for nestling A. I tested for differences in rates between the two nestlings by using values for the observation time to calculate expected values for frequency of occurrence. The difference in rates was not significant.[18] (Figure 21).

Koford (1953, p. 112) reported that California condor nestlings tended to be active shortly after sunset. The trend was also true for both nestlings 2 and A. Avoiding exposure to the sun would not explain this schedule for activity by Nestling 2 since the nest was never in the sun during the period of observation. Activity by both *Vultur* and *Gymnogyps* nestlings was marked just after a feeding. One post feeding bout of activity by nestling 2 occurred with the adult male still on the ledge, another while the parent was inside the cave.

Begging

In bouts of begging by feathered nestlings the movements of flapping and head bobbing varied markedly both in degree and frequency. Usually the bird squatted, flapped partly extended wings about twice a second and bobbed the head up and down 1 to 10 cm. Sometimes, however, legs were flexed only very slightly, wings jabbed away from the body irregularly, and only a few centimeters, and the head moved little. Even though the intensity of motion was variable, wing movement in begging followed a basic pattern. As in the wingbeat of the airborne condor the wing generally moved in a dorsoventral direction, with the cycle of up and downstroke by the brachium preceding that of the antebrachium and the cycle of the antebrachium preceding that of the manus. In the begging wingbeat, however, both elbow and wrist were strongly flexed, and this distally oriented lag in the cycles of movement by the three parts of the wing was more pronounced, producing a whiplike motion. During intense bouts of begging, the elbows struck each other above the back.

Usually, legs were flexed enough so that the breast almost touched the ground, and the tail was elevated to an angle about 45^{o} above the long axis of the body. Although the head remained level, it bobbed vertically in rhythm with the wingbeat, ascending when the antebrachium and manus descended. Sometimes the chick walked or turned in circles while begging. Slower, shorter movements of wing and head often occurred when the bird did not squat.

Nestlings begged only when the parents were present, either at the nest or in the air nearby. Usually, begging commenced 2-3 seconds before a parent landed, although several durations of 3-4 minutes were recorded before the adult alighted. Once AF2 circled for 2 minutes in front of the nest, and the nestling watched her but did not beg until she landed. Sometimes the chick begged for a few seconds when an adult female landed on a rock 1 m above him. He began to beg vigorously, when she jumped down to him. Feeding followed immediately. Usually, the nestling continued short burst of beggin motions during the feeding bout. The breast of the nestling touched or almost touched the ground, and the tail was elevated; the young bird often shuffled in half circles around the parent. The manus of the chick frequently struck the ground. At times the head of the feeding parent was caught in the primary and secondary wing feathers of the active youngster. Once, I noted that the rate of wing movement by the nestling was somewhat less than that of the neck-pumping action of the feeding. After a feeding bout, the nestling usually followed the adult about on the ledge or in and out of the cave; begging often continued. After one feeding nestling 2 continued to beg and follow the parent even though the crop of the young bird was very full.

Some adult activities at the nest seemed more closely associated with begging by the chick than others. When the adult preened the nestling, begging was rare; yet the chick often begged when the adults wiped their head and neck or just before and during take off. After the

adult flew, the chick sometimes begged for several minutes. The nestlings usually resumed a normal stance after begging but occasionally stood with wings drooping, so that the wingtips were on the ground, and the wrists sagged 10 to 30 cm below their usual position.

Nestling 2 begged in captive conditions. The condor was captured a week after leaving the nest and begging was first observed 12 days later. The bout preceded feeding and occurred when the condor was shown food. Later, begging frequently occurred when food was not present. Each bout was usually preceded by a low rattling vocalization. At 5.5 years, the age of this bird when he was donated to the San Diego Zoo, the condor continued to beg on nearly a daily basis when I approached him. The frequency and intensity of the pattern seemed directly related to how long it had been since the last feeding.

Shortly after his capture I noted that wing movement by the begging youngster demonstrated a peculiar orientation to my approach. When I approached on his left side, only his left wing flapped. When I walked toward the right side, only his right wing moved, and when I approached him head-on, both wings flapped to the same degree. The orientation might be useful to young condors perched on a narrow ledge. Movement on the side of an approaching adult would help the parent locate the volant juvenile. Flapping the wing facing the cliff would contribute little to ostentation and might push him from the perch.

Sunning

Most of the sunning postures observed for nestlings were by nestling A. Nest 2 was never exposed to the sun during the period of observation; only once did I see nestling 2 stand motionless with wings outstretched for an extended period; he held the stance for 11 minutes. In contrast, nestling A sunned frequently. I recorded 17 instances by this chick, all of them during hours before 1300. Between 1200 and 1300, the sun's rays left the nest area until sunrise the following day. Although I saw one instance as early as 0657, preferred hours of sunning

appeared to be from 0800 to 1000, when nearly two-thirds of the 17 bouts occurred, a significant proportion (Table 24).

Bouts of sunning by young condors were less extended than those of adults. Durations recorded for nestling A were usually around 1 minute, approximately the same observed for immature condors, while those of adults tended to be at least twice as long (Figure 7). Like adults, nestling A oriented the dorsal surface of her wings to a position perpendicular to the sun. In the morning, the sunning chick held her wings so that the chord axis of the wings was about 90^{o} with the horizon, whereas it was parallel at midday. Usually, the nestling sunned facing toward the cave; occasionally she faced the canyon, and several times she stood sideways in the cave entrance. Once, exposing only the left wing to the sun, she stood this way for 4 minutes. Then she turned 180^{o} and, exposing only the right wing, sunned for 1 minute. Intervals of flapping often interspersed bouts of sunning. Sunning frequently ended when extended wings drooped to the ground, sagging, at times, for intervals of up to 1 minute.

Stretching

In general, but the bow and side stretch of nestlings were similar to those of adults. Variation in some minor elements characterized nestling patterns; adult forms were more consistent. Sometimes nestlings elevated one wing and then the other in the bow stretch. On occasion they walked about during the pattern. Stretching often occurred during periods of flapping and leaping activity. Side-stretching patterns observed for nestlings were more protracted than those of adults. Four durations recorded for the nestlings ranged from 13 to 18 seconds, whereas most of the adult patterns were around 9 seconds. The sequence of motor patterns in the side stretch by chick and adult were the same, although restricted space around the nest modified a few patterns. In several side-stretch and one bow-stretch patterns at the cave entrance, only the wing facing the canyon was extended; the other remained flexed. Stretching

Table 24. Occurrences of sunning by nestling A and the time of day. Data recorded from 15 April 1969 to 29 April 1969.

	Time of Day								
	0500-0659	0700-0759	0800-0859	0900-0959	1000-1059	1100-1159	1200-1259	1300-1830	Total
Observed no. occurrences	1	0	6	5	2	2	1	0	17
Expected no. occurrences[a]	0.7	1.5	1.6	1.5	1.5	1.5	1.5	7.3	17.1

[a] Calculated using the proportion of observation time for each hour.

Note: Differences are significant considering three periods: 0500 to 0959, 1000 to 1259, 1300 to 1830, $\chi^2 = 15.98$, df=2, $p<0.001$

occurred throughout the day. I searched for but found no association between the frequency of stretching and the hour of the day.

Postures of Threat and Attack

Assuming that the parents had abandoned the nest, I took a young condor captive. During the capture and the early hours of the following day, the condor assumed threat postures whenever I approached him; several times he attacked. In the threat posture, the long axis of the body was more horizontal than usual, forming an angle of 30^{o} to 45^{o} with the horizontal. Head and neck extended horizontally. The tail remained parallel to the long axis of the body. Wing coverts and back feathers were erected. Intervals of less than 1 second separated hisses 4-6 seconds in duration. His beak was open about 5 m at the tip and the tongue extended to the distal end of the inside of the beak. Wings were elevated over the back. He partially extended the elbows and flexed his wrists flexed, so that the wingtips remained near the tail. Except for the marked flexion of the manus, the position of the wings resembled that of the courtship posture, a similarity also noted for captive birds by Gailey and Bolwig (1973). Koford (1953, p. 80), as well, noted a likeness of threat and courtship attitudes by *Gymnogyps*. In the threat posture of the nestling turkey vulture, the wings are extended with the wrists bent, so that the wingtips touched the ground (Davis, 1979); in attack, the young turkey vulture jumped forward and snapped its beak. The bird regurgitated if just fed. Similarly, in the attack, the young *Vultur* extended his neck sharply, leaped forward by extending both legs simultaneously, and bit at me. Motions of the attack were the most rapid I ever saw the bird make. After I held him down a dark foul-smelling liquid discharged from his beak. Air sacs in the neck were expanded, and he continued to hiss. The postures of both threat and attack disappeared at the end of the following day after I sat with him in a darkened room for about 8 hours.

Other Behavior

As with adults, preening was the most frequent activity of the nestlings. Nestling 2 often stood out on the ledge and preened for periods that ranged up to 15 minutes. Sometimes when he preened wing coverts, his wrist extended forward about 10 cm from the usual position. Occasionally, the extended wrist dropped 10 to 15 cm, while the tip of that wing ascended from 2 to 30 cm above the base of the tail. When preening activity moved from the wing to another part of his body, the wing often continued to sag away from his body. Usually, it was reset in less than a minute. Patterns of preening in other areas of the body seemed no different from those of adults.

Posture and movements of the head scratch pattern also resembled those of the adults. The scratching movements recorded in two bouts by nestling 2 were 18 and 10. I never saw a nestling wipe the head and neck on the ground as the adults did, although several months after his capture, the immature male condor began wiping his head and neck after most feedings (Plate 10). Exploratory nibbling by nestling 2 occurred in sitting, standing, and lying positions. He frequently nibbled at stems and leaves of plants that grew on the ledge in front of the cave entrance. I never saw nestling A manipulating objects with her beak; vegetation in the vicinity of that nest was absent.

CONCLUSIONS

Whereas California condors usually nest only every other year, Andean condors in equatorial regions might nest every 18 months if the juvenile survives. The onset of breeding seems keyed to the start of the rainy season in April or October. A cycle of this duration is possible, even if the period of juvenile dependency in *Vultur* is an extended as that of *Gymnogyps*. Several conditions indicate a briefer period of dependency for *Vultur*, which allows the possibility that *Vultur* could breed annually at any latitude of its range.

Both sexes of the Andean condor court but some differences are notable. First, males courted more often than females. Second, females usually flapped their wings, whereas the males did not. Courtship postures by the female usually lasted longer than those of the male. In sum, females tended to court less than males, but they did so with more animation and for longer durations. Courting may help to synchronize a physiological readiness for reproduction between the sexes. If so, testicular development in the male for a successful fertilization could extend over a longer period than ovarian development in the female, where only one egg is normally produced. Male courtship, indicating a physiological readiness, might operate at a lower level of intensity and over longer periods than that of the female. If insemination must occur at a relatively short period in the breeding cycle of the female, intense and long bouts of courting by her might serve to ensure fertilization at that time. Behavior of nesting pairs supports this hypothesis, in that the male often courted, whereas the female did not. Yet courtship by the non-nesting female of pair 1 and by females in Paracas indicates that if a readiness for nesting exits, the period before laying must be extended, as we were unable to find any evidence of nesting by pair 1 during nearly four months of observations or by any of the condors on Paracas.

Courtship postures, with only a few rare exceptions, occurred only in the presence of an adult of the opposite sex and, in each of 15 instances where activity prior to copulation was observed, the bird mounting performed a courtship pattern beforehand, usually immediately before mounting. Condors tended to court and copulate during midday period from 1100 to 1300. Sexual activity was suppressed in the morning from 0600 to 0800 and in the evening from 1700 to 1900. I found no variation in levels of sexual activity in 11 sampling period of distributed over nearly four months.

Both sexes of Andean condors were seen to mount. The full copulation sequence seemed identical, regardless which bird was where, and indicates that sperm transfer might also occur in

female-mount-male patterns. Threat postures observed in a few instances were similar to the courtship posture, except that the neck and head were not pointed downward. Threat and courtship postures for *Gymnogyps* are also similar to each other and to those of *Vultur*. *Vultur* appears to participate in sexual activity more than *Gymnogyps*; the number of copulation patterns observed in Koford's study was much smaller than those recorded in this search, both in absolute terms and in relative terms, where I used the number of courtship postures observed as a baseline.

The sexual activities of courtship and copulation in the Andean condor appear to be more than seasonal or periodic phenomenon and suggest that sexual relations serve more than the narrowest function of reproduction. Courtship occurred regularly throughout the late nesting stage of pair 2, a case where egg production for that season had already been completed. I observed courtship by the non-nesting pair over a period of almost four months from 17 November 1968 to 7 March 1969 and copulation postures during a 1-month period from 27 November to 12 December 1968. I doubt they incubated an egg for at least three months afterwards, however. Both courtship and copulation postures may have continued to occur at the same rate, but the pair frequented the observed roost area less often, so I could no longer follow their activities. Mates of pair 1 might have been the two birds observed copulating at the bait on 1 October 1968, an instance that would extend the period of copulation postures observed for them to almost four months.

Other observations also indicated extended periods of sexual activity. William Millie and I observed an apparent copulation in Chile near the village of Chañarel on 31 July 1969. According to egg records for central Chile (Table 10) this sexual interaction occurred from one to three months before the usual laying period. Condors visiting Isla Zárate in Peru were members of a transient population that were unlikely to be nesting at the time; nonetheless, I

observed seven copulation postures from 11 October to 31 December 1969. Moreover, I always saw a courtship or copulation behavior on the island if I observed a number of condors there for several days. Adults visiting the island tended to travel in male-female pairs, a topic discussed later (see Appendix C); sexual activity might have characterized mate relations of these pairs as part of a long-term relationship that included a nest in the cordilleras during one part of the breeding cycle and migration to the coast during another. A pair of captive Andean condors at the West Berlin Zoo were observed to display in December, copulate in January, and lay an egg in March or April for five consecutive years (Klös, 1973); here, interims of two or four months spaced instances of observed copulation and egg-laying.

Sexual activity that promoted and perpetuated strong pair bonds for periods before and after the nesting season would provide gains beyond the insurance of a mate. Coordination of joint activities, foraging in particular, probably improves as the period of association grows longer. The umbrella of male dominance could shelter his mate and provide her with an access to food superior to that of unmated females and, depending on her mate's position in the hierarchy, to some males. Year-round health of the egg-laying female is important to both members of the pair, as is any advantage the pair garners for provisioning the young.

Nesting mates spent less time with each other than the mates of non-nesting pairs. Additional demands for food might separate foraging and roosting habits of adults in the late nesting stage, so that more territory can be covered. Some foraging independence might also stem from individual efforts at providing a consistent feeding schedule for a nestling; one may return to the nest with food, while the other continues to search for more. Pair bonds of nesting adults are no doubt reinforced by the common interest in nest attention. In comparison, non-nesting pairs might attend to each other to a higher degree when the responsibility of a nest is absent, either in an active sense, to establish an enduring pair bond, or passively, as a

consequence of the difference in feeding pressures.

Before departing from the roost area, parents often fed chicks at both nests; onset of foraging usually began between 0800 and 1000. Food provided in the morning would have been available the preceding evening. Feeding may be scheduled by the parents to provide the most consistent timetable for the chick. Roosting adults retain a quantity of food for digestion during the night. Feeding the remainder in the morning would provide more room in the crop for additional food, as well as lighten the weight of the foraging adult.

Parental behavior by *Vultur* seems to differ significantly from that of *Gymnogyps*. California condors observed by Koford did not roost in the immediate nest area, as did the Andean condors we observed, nor did they frequent the nest as often or as long. Food may have been more distant for *Gymnogyps,* or the adults may have been responding to the presence of Koford even when conditions outwardly seem undisturbed. None of the members of pairs 1,2 and A appeared to respond to my frequent presence 0.3 to 1.5 km away on the other side of the Rio Pasto canyon. Perhaps the difference in parental behavior by the two species can be attributed to the fact that few activities of the Colombian condors ever occurred farther from humans. By way of natural selection or short-term habituation of individuals, all or most responses to humans may have waned for these short distances. In general, the nesting areas we observed appear more inaccessible to man than those used by California condors; thus, the presence of humans in the nest area of *Vultur* may present a relatively smaller threat.

Owing to their great size and to the special problems of flight such a size entails, juvenile condors are particularly dependent on post-fledging care from their parents. We saw sub-adult condors 5 and 6 years of age that still had not mastered flight maneuvers with the smoothness that adults demonstrated. In all likelihood, juvenile condors are often caught in winds that carry and strand them some distance from the site of a previous encounter with a parent. Parental

demands of this extent are likely factors in the evolution of the low productivity characterizing both species of condors. The difficulties in caring for two or more young would probably result in fewer viable offspring then when parental efforts are channeled to one juvenile (see Amadon, 1964).

CHAPTER 5. SOCIAL BEHAVIOR

INTRODUCTION

The primary goals in this chapter are a description of the patterns of interaction; segregation of distinctive behavior trends for the relationships among certain individuals, within and across the different sex and age classes, and for different populations; and a definition of the basic principles of structure around which the social organization of these large vultures has developed.

In one section of this chapter I define and describe each pattern of interaction observed and provide the quantitative data recorded for its frequency and rate. Another section focuses on relationships observed at feeding areas, and one other part with those of the perch and air. In the last part of the chapter ,characteristic trends in these relations are described for (1) transient populations on the south Peruvian coast and the more resident population in Colombia, (2) different sex and age classes, and (3) different individuals. The subject of dominance and its determinants is considered here in some detail in an attempt to define the funamentals of social organization.

Vultures are prime subjects for studies of social behavior because typically, their existence is carried forth in and around groups. Unlike most of the socially independent raptors, vultures tend to associate with each other in the air, on perches, and at feeding sites. Carrion, the usual food source of the vulture, appears in large and scattered quantities and deteriorates rapidly. Although it might be useful for a hawk to defend a small prey item from another hawk, it would be of little value for a vulture to defend any enormous mass of carrion the bird cannot use alone. That is not to say that vultures do not compete for food; competition does exist but in closer physical proximity than that of the hawk or eagle. Competition for food among the

vultures of a region ordinarily occurs in certain feeding area on a daily to weekly basis and often involves repeated encounters among the same individuals.

The Andean condor is one of the most ideal subjects for a detailed study of scavenger social behavior. Sex and age classes are easily identified for condors either perched or aloft. Population densities are relatively low, and individuals can often be distinguished. Tempos of activity are relatively low for a bird, so it is easy to observe individual patterns of interaction and to measure associations and rates of interaction.

We watched for condors from blinds constructed near baits for about 1100 hours; 800 hours in Colombia, 180 hours near Paracas, and 120 hours in the Cerro Illescas. Condors were present at those baits put out about 5 percent of that time. In addition, from the tip of a peninsula near Paracas, we watched condors on the island Isla Zárate for about 100 hours (Figure 4). We recorded most of the data describing relationships on the perch and in the air during another 320 hours of observation at a roost and nest area in Colombia. Information on feeding relations came primarily from Isla Zárate and the baits in Colombia. Groups at the Colombian baits usually comprised two or three birds but included up to seven at times, whereas group size was generally larger on Isla Zárate and ranged up to 17, with the majority from two to ten. At the perch and in the air, groups tended to be smaller than those of the feeding sites.

PATTERNS OF INTERACTION

Associations at Feeding Areas

Analysis of Durations Between Bait Arrivals

The probability of a condor landing near a bait carcass at a given time seems to increase if another condor is already there. Positive associations between condors at the feeding area are evident; 97 percent of the intervals separating arrivals by the first and second condor were less

than 15 minutes, even though condors were present at the bait only about 5 percent of the daylight time. To detect possible time-related differences in the probability of arrival by a second condor, I examined the distribution of intervals separating the arrivals of the first two condors. I excluded intervals for those instances where the first condor took off before another landed; the presence, not the actual landing, of the first bird would probably enhance the arrival of the second. The distribution obtained in plotting the logarithms for cumulative frequency of intervals between first and second arrival against interval duration (Figure 22) indicates that the probability of arrival of a second condor was greater 0 to 6 minutes and 10 to 15 minutes following arrival of the first condor and smaller 6 to 10 minutes and 15 to 34 minutes subsequent.

Condors may have foraged in groups or they may have approached the area independently and then circled nearby, alighting only after a less cautious condor landed first. In these 88 observations I found that the visitation duration or time at the bait by the condor arriving first was significantly correlated with the interval durations separating the arrivals of the first and second birds (Figure 23). So the condor that arrived first tended to visit the bait longer when intervals separating another's arrival were more prolonged. The relationship suggests that the arrival or presence of a second bird hastened the departure of the first.

Analysis of Social Context at the Bait

When groups of condors frequented the bait, neither the (a) sex and age class nor (b) the individual composition of these groups appeared random. As an example of the latter, IM3 was accompanied by a second condor at the bait for a total of 513 minutes; of at least eight individuals involved as the second condor, one alone, IM2, shared two-thirds of that time. Some of the trends were class-specific: Adult males fed alone 58.5 percent of the time, compared to 28.1 percent for immature males (Table 25).

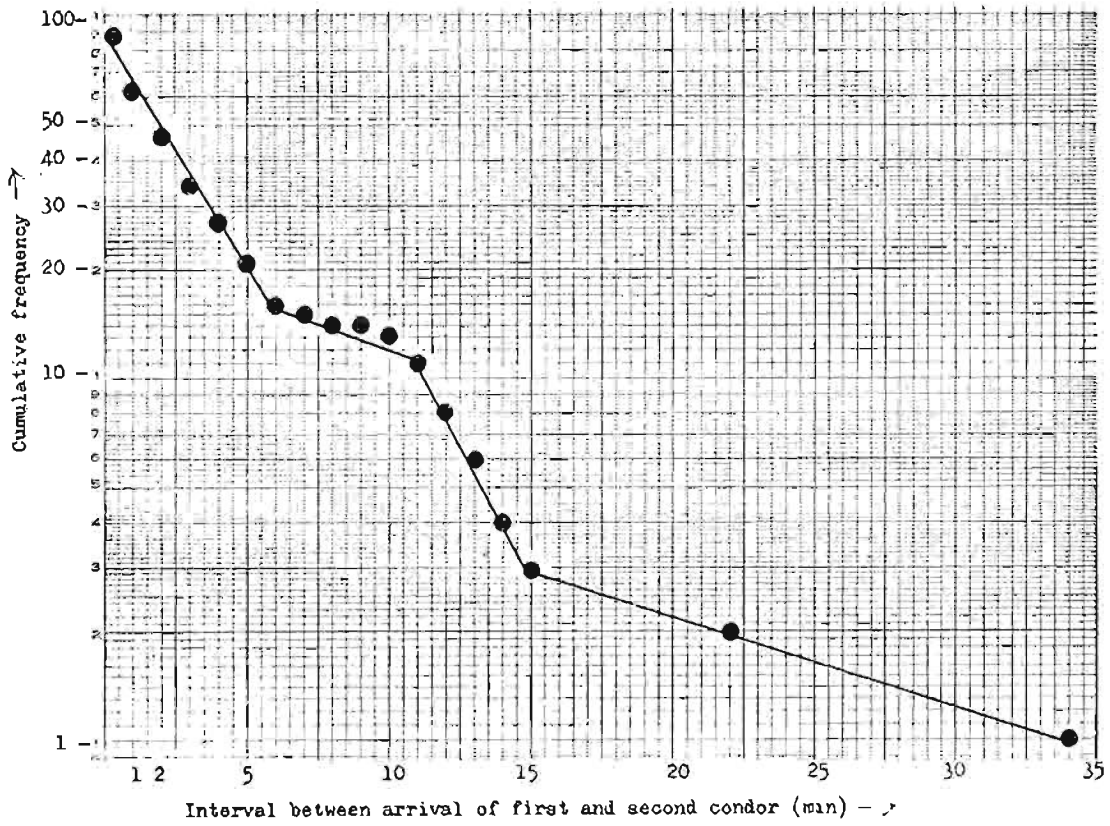


Figure 22. Logarithms for cumulative frequency of intervals separating arrivals of first and second condors at the Colombian baits plotted against interval duration (n=88).

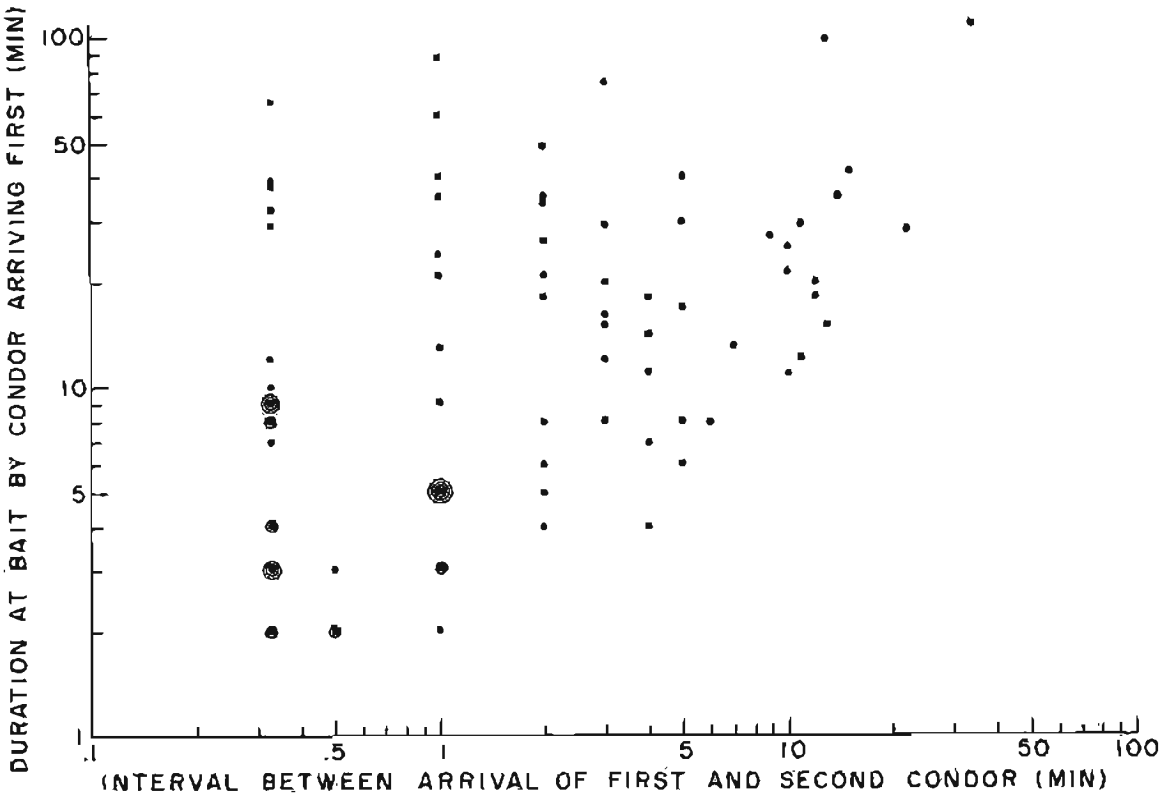


Figure 23 Relation of the interval duration between arrivals of the first and second condor and the time spent at the bait by the first condor (n=88, r=+0.28, p<0.01, Y=13.0 + (1.83X). Plotted on logarithmic axes for display.

Table 25. Visitation and feeding durations for condors at the Colombia baits recorded from 1 October 1968 to to 15 March 1969.

Sex and age class->	Immature Male				Immature Female			Adult Male					Adult Female
Individual designation->	1	2	3	Total	1	2	Total	1	2	3	4	Total[a]	Total
Total visitations recorded	14	60	47	155[a]	11	10	21	19	25	29	17	167	145
Total feeding bouts recorded	16	74	86	200	25	11	36	17	19	30	13	132	136
Total min recorded for all visitations	326	1195	1542	3420	378	165	542	92	164	285	82	1068	1269
Total min recorded for all feeding bouts	125	704	878	1912	228	83	311	62	83	180	50	666	719
Mean and computed standard error for duration (min) of:													
visitations	23.3±5.7	19.9±2.6	32.8±4.5	22.1±1.9	34.3±10.0	16.5±5.1	25.8±6.0	4.9±1.3	6.6±1.3	9.8±1.5	4.8±1.6	6.4±0.5	8.8±0.7
feeding bouts	7.8±2.0	9.5±1.1	10.2±1.1	9.6±0.7	9.1±2.6	7.6±2.8	8.6±2.0	3.6±0.7	4.4±0.8	6.0±1.2	3.8±0.7	5.0±0.4	5.3±0.4
Coefficients of variability													
visitation durations	92	102	95	108	97	98	106	119	101	84	110	107	100
feeding bout durations	105	97	101	99	142	123	137	83	81	105	94	93	88
No. observation days during which durations were recorded	8	21	21	27	5	5	10	7	11	14	4	36	40
Percent of visitation time accompanied by:													
no other condors	13.4	10.4	19.7	17.1	40.9	3.9	29.9	0.0	48.2	20.3	18.8	24.2	24.8
1 other condor	15.7	37.7	33.3	32.2	28.1	29.7	28.5	33.7	11.6	21.4	63.5	27.6	28.4
2 other condors	51.9	33.0	31.9	32.7	21.2	29.4	23.7	6.4	22.1	29.9	17.7	23.2	23.8
3 other condors	11.6	14.7	12.1	13.7	9.8	35.8	17.5	44.9	11.9	21.7	0.0	18.1	15.0
4 other condors	5.8	3.8	2.8	3.4	0.0	1.2	0.4	15.0	3.4	6.8	0.0	5.8	5.8
5 other condors	1.5	0.4	0.3	0.8	0.0	0.0	0.0	0.0	2.8	0.0	0.0	0.9	1.5
6 other condors	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.7
Percent of feeding time accompanied by:													
no other feeding condors	5.3	28.3	29.6	28.1	52.6	44.9	50.8	51.6	68.8	59.4	67.3	58.5	52.0
1 other feeding condor	23.9	45.9	46.6	43.9	37.3	34.6	36.7	24.2	26.9	16.5	32.7	28.2	32.7
2 other feeding condors	62.8	23.4	21.2	24.0	7.6	20.5	10.7	4.8	3.2	15.3	0.0	7.1	12.0
3 other feeding condors	6.2	2.2	2.3	3.7	2.4	0.0	1.8	19.4	1.1	8.8	0.0	5.8	2.9
4 other feeding condors	1.8	0.3	0.2	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.3

[a] Includes members of this sex and age group that are unidentified individually.

In addition to the information on feeding characteristics of different individuals and classes that is presented in Table 25, I secured some data on associations by comparing values on the percentage of visitation and feeding time of particular individuals or classes in groups of differing size. Meaningful probability statements for the comparisons are difficult to obtain, however, because the constellation of birds at the bait recorded for each sample minute likely has some dependent relationship with the status in the preceding and succeeding minutes.

In another approach to the description of associations, I constructed a contingency matrix to compare the frequency of arrivals at the bait for different individuals and classes according to the class and number of birds already present (Figure 24). To compare observed and expected frequencies for each category or cell I compressed the remainder of the matrix and performed a two-sample chi-square test (see p. 69). Similar analyses of association were conducted on the frequency of departure from the bait in the context of the class of condors present, and on the onset and cessation of feeding according to the class of condors feeding at that time (Figure 24). Data from two situations were not used in these analyses: (1) Usually all the black vultures and condors at the bait flew at once when a black-bellied buzzard-eagle (*Gerancaetus melanoleucus*) flew over the area, and (2) occasionally two birds landed, took off, began feeding or stopped feeing simultaneously. Results from this method of analysis are discussed in the section that examines relationships among condors at food.

Associations in the Air

Certain condors were often seen flying together. In Colombia, for example, two immature males (IM2 and IM3) foraged extensively with each other. Among adults, birds of opposite sex tended to travel together. To test for sex associations between foraging adult condors in the Colombia study area, I compared the frequency of observations for two adults

(1) ARRIVING

↓ PRESENT	Immature male	Immature female	Adult male	Adult female	Total
no condors	0.12 50	9.93 + 14	8.32 − 42	3.70 58	164
1 immature male	12.54 + 32	1.39 1	10.90 − 10	0.13 20	63
1 immature female	1.98 8	0	0.01 6	1.25 3	17
1 adult male	0.30 5	0	4.19 − 1	3.69 7	13
1 adult female	0.02 10	1	8.57 + 19	7.28 − 3	33
>1 condor	7.69 − 44	2.05 5	18.00 + 84	0.88 50	183
	149	21	162	141	473
More than 1 condor present					
≥1 immature male(s) included	5.59 − 40	1.10 5	16.92 + 76	1.94 42	163
no immature males	1.28 4	0	0.31 8	0.03 8	20
≥1 immature female(s) included	3.82 11	2.89 0	7.67 + 28	0.02 16	55
no immature females	2.66 33	0.11 5	7.03 + 56	0.88 34	128
≥1 adult male(s) included	0.01 12	2	1.40 10	1.52 15	39
no adult males	8.26 − 32	2.71 3	27.01 + 74	3.00 35	144
≥1 adult female(s) included	0.05 25	2.42 1	6.44 + 38	2.93 18	82
no adult females	9.58 − 19	0.07 4	7.28 + 46	0.22 32	101

(2) DEPARTING

↓ REMAINING	Immature male	Immature female	Adult male	Adult female	Total
	11.35 + 54	0.38 7	4.20 − 45	1.87 39	145
	7.21 + 24	0.05 2	1.68 17	1.30 14	57
	0.49 2	0	1.41 6	0.07 3	11
	6.76 − 0	0	10.67 − 0	39.66 + 17	17
	0.49 2	0	6.02 + 8	2.54 1	11
	14.71 − 20	0.17 6	10.33 + 63	0.03 41	130
	102	15	139	115	371
	13.07 − 17	0.63 6	9.54 + 56	0.01 35	114
	0.64 3	0	0.28 7	0.33 6	16
	2.91 6	0	14.50 + 25	3.13 7	38
	9.25 − 14	1.94 6	0.77 38	2.03 34	92
	2.62 6	1	3.03 9	12.75 + 21	37
	9.63 − 14	0.57 5	22.48 + 54	5.23 − 20	93
	4.29 − 7	5	1.20 21	0.04 14	47
	7.51 − 13	2.22 1	7.88 + 42	0.12 27	83

↑ ALREADY FEEDING

Figure 24a. Distribution of (1) arrival and (2) departure frequencies at bait according to the number and sex and age class of condors arriving or departing and those already present or remaining, and the frequency of occurrence for (3) the onset and (4) cessation of feeding at the bait by condors of different age and sex classes that already are feeding or remain feeding. Chi-square values are listed for those categories with expected frequencies exceeding two. Substantial departures (over 3.84) are framed with heavy lines and the direction of departure noted. See page 121b for an overlapping continuation of this figure.

PARTING

(3) COMMENCING FEEDING

(4) STOPS FEEDING

Adult male	Adult female	Total	Immature male	Immature female	Adult male	Adult female	Total	Immature male	Immature female	Adult male	Adult female	Total
4.20 − 45	1.87 39	145	15.50 − 64	1.23 13	13.05 + 82	0.00 69	228	5.56 − 62	0.36 13	8.11 + 79	0.58 62	216
1.68 17	1.30 14	57	28.37 + 32	2.57 0	15.46 − 2	0.82 11	45	5.84 + 22	1.06 1	6.01 − 7	0.26 15	45
1.41 6	0.07 3	11	2	0	2	0	4	1	0	4	0	5
10.67 − 0	39.66 + 17	17	0.31 4	2	6.07 − 0	4.99 + 8	14	0.50 2	1	4.22 − 0	5.88 + 6	9
6.02 + 8	2.54 1	11	5.52 + 12	0	1.14 8	9.19 − 0	20	2.16 8	1	1.21 7	7.24 − 0	16
10.33 + 63	0.03 41	130	1.23 13	0.02 2	0.77 11	4.38 + 20	46	0.27 14	0.00 2	4.81 − 6	2.95 16	38
139	115	371	127	17	105	108	357	109	18	103	99	329
9.54 + 56	0.01 35	114	0.80 13	0.69 1	0.47 11	3.98 + 19	44	0.28 13	2	5.28 − 5	3.03 15	35
0.28 7	0.33 6	16	0	1	0	1	2	1	0	1	1	3
14.50 + 25	3.13 7	38	1	0	1	1	3	1	0	1	1	3
0.77 38	2.03 34	92	1.25 12	0.00 2	0.89 10	4.50 + 19	43	0.28 13	2	5.28 − 5	3.03 15	35
3.03 9	12.75 + 21	37	4.52 − 0	1	3.41 0	12.71 + 7	8	1.60 6	0	3.06 1	0.79 5	12
22.48 + 54	5.23 − 20	93	0.03 13	1	0.00 11	0.32 13	38	0.07 8	2	1.91 5	2.00 11	26
1.20 21	0.04 14	47	1.45 4	1	0.00 2	3.10 0	7	0.53 4	0	2.53 5	3.98 − 0	9
7.88 + 42	0.12 27	83	2.98 9	1	0.85 9	9.18 + 20	39	0.03 10	2	11.48 − 1	9.51 + 16	29

← ARRIVAL FEEDING →

← REMAINS FEEDING →

Figure 24b. An overlapping continuation of Figure 24a on p 121a.

flying within 300 m of each other with expected values computed from figures on the total number of observations of adult males and female in flight, either alone or with other condors (Appendix B). Adult male-adult female pairs were observed flying more often than expected and within sex class pairs less often. In contrast, the relationship was not significant for a similar test on condors flying across the Peruvian beach, Playa Chucho, during the flight study (Appendix B). In yet a third comparison, however, on condors crossing the Zárate channel 18 km north of Playa Chucho, we saw significantly more adult male-adult female pairs than expected, which suggest that pair bonds remain strong in locations far from the nesting area (see p. 114 and Appendix B). The difference recorded in aerial association on these two parts of the Peruvian coast may have been due to seasonal changes in social behavior during different sampling periods or to topographical effects on the coordination of flight patterns for two birds foraging together.

Social Postures

I saw certain postures occur only when two or more condors were present. In some instances, the posture appeared in only one or two particular settings, an indication that it served as a communication signal. One particular wing-extended pattern, the courtship posture, was the most common social posture noted. The pattern occurred in sexual encounters and is described in detail in Chapter 3 on reproduction. It occasionally appeared in other settings, sometimes in the presence of members of the same sex and age class. Situations where the posture appeared to serve as a threat are discussed on p. 83. Kruuk (1967) reported threat postures by the lappet-faced vulture, in which the bird approached in an erect stance, bill pointed downward, and wings half-spread. Intermediate postures also occurred between this and another posture in which the body was horizontal, neck feather raised, and the wings fully extended. The first stance

resembles the courtship posture of the Andean condor.

Sunning postures of the condor often occurred in group situations and may have had some communication function. Condors often began or ceased sunning at the same time. Sunning durations for two adults pairs observed in the same area were significantly different between but not within pairs (p. 56); social factors may have influenced the timing.

A change in the shape of the neck characterized some courtship patterns and aggressive encounters. In a number of these interactions the crop region of one condor expanded, and the bare skin became more yellow or red (Plate 14). Distended with meat, the crop expands at the base; but in the instances noted above, the crop region appeared swollen in the upper part as well, probably with air. In aggressive encounters, these neck changes usually characterized the attacker. The crop region of one adult female, for example, became swollen just after she chased another adult female off the bait. According to Todd (1974), the neck diameter of a captive *Gymnogyps* nearly doubled when it was inflated with air. In the male Marabou stork, a large pink throat sac becomes conspicuous after mates establish a nest site; when fully inflated, the sac hangs down 30 cm or more (Kahl, 1966). As noted earlier, storks are probably close relatives of New World vultures.

Attacking and Fighting

Description

An attack is defined here as a sudden running or bounding movement with a pecking motion directed toward another bird. Supplanting patterns 7-10 listed in Table 27 (see p 125a) are all considered attacks. Usually, an attacking condor bit and held the skin on the top of the other's head or neck, while the attacked condor ran backwards in an erect posture with wings flapping. Sometimes the attacking bird jumped upon the other's back and bit at its neck or back.

Plate 21. An adult male approaching the bait with his crop in an expanded position. And adult female retreats from the bait in the foreground (left). The expanded crop often appeared in aggressive or sexual encounters.

Responses by attacked condors varied; many simply ran or pulled away. Frequently, one condor gripped by another would place a foot on the breast or side of the attacker and push him away. A more gentle variety of the push-away pattern often terminated the head nibbling interactions. In some instances of attack stereotyped postures were assumed. IM2 once responded to blows from another condor by standing erect with his head tilted up at a 45^{o} angle and his beak open. He stretched his neck up and forward. An adult female with wings partly open had jumped at him twice striking him with her feet; she did not peck at him. An adult male (AM3) at the bait responded to the landing and running approach of another adult male (AM1) by crouching, opening his beak, and holding his neck near the ground with the head tilted up in a posture like that of a begging chick (Figure 18). The attacking male, with wings extended, pecked at and touched the beak of the crouched bird. The attacked male made a weak pecking motion in response. Then the attacking male turned, folded his wings, walked to the carcass, and fed.

A contested fight between condors began when an attacked bird pecked back. Fights usually involved pecking, jumping, and flapping by both birds (Plate 15). Fights ended abruptly and often lasted no more than 10 or 15 seconds. One bird ran or flew with the other in pursuit; sometimes the fighting suddenly stopped, and both birds stood motionless 1 or 2 m apart and then, usually after 1 or 2 minutes, one bird walked away.

Table 26 tallies the number of contested fights observed according to the sex and age class of participants. These data are discussed in Section 3.

Function of Fighting

Fighting may serve to establish unidirectional dominance for supplanting on a later encounter. Another possible function of fighting or attacking is to force another bird to regurgitate. Several times I saw a member of a quarreling group of black vultures suddenly

Table 26. Frequency of contested fights. .

Sex and age class	No. of fights		No. condor hour for observations at feeding area when:		Freq. interclass fights/condor hour when 1 or more interclass condors present	Freq. intraclass fights/condor hour when 1 or more intraclass condors present
	Inter-class	Intra-calss	1 or more members of another class also present	2 or more members of the same class are present		
Colombia-baits						
Immature	2	4	27.1	48.9	0.07	0.08
Adult male	0	2	13.5	1.1	0.00	1.82
Adult female	2	0	15.6	2.9	0.13	0.0
Peru-Isla Zárate						
Immature	4	0	44.2	41.3	0.09	0.0
Adult male	3	5	82.4	66.4	0.04	0.08
Adult female	5	4	117.3	123.1	0.04	0.03

Interclass fights: Colombia, adult female-immature male = 2; Peru, adult male-adult female = 2, adult female-immature male = 3, adult male-immature condor = 1. In this comparison immature males and immature females were grouped in a single class.

Plate 22. Two adult males fighting at the bait in the Colombia study area. A contested fight like this occurred when an attacked condor pecked back. Courtesy of the National Geographic Society.

disgorge and take off. The regurgitated food was quickly eaten by the other vultures. Frequently, a third black vulture entered a fight between two others, a useful intervention, if one bird could be forced to disgorge. Sometimes California condors fight in groups of three (Koford 1953, p. 32). I saw three Andean condors fighting together for a moment in two separate instances -- once with three adult males and another time with two adult males and an adult female. Although I never saw a quarreling or attacked condor disgorge, one observation suggests it might occur: IM3 ran from the carcass shaking his head from side to side, apparently choking; IFl immediately left from where she fed, pursued the male, and pecked at his head. They passed out of view of my blind, so I was unable to see if the male disgorged.

Supplanting

Classification of Patterns

The most conspicuous interaction at the feeding area was the displacement of one bird by another from a feeding point on the carcass. For condors visiting the baits in Colombia and the beaches of Isla Zárate in Peru, I recognized 10 discrete types of supplanting behavior (Table 27) and recorded their frequency according to sex and age class (Tables 28 and 29). Likewise, when recording responses to supplanting approaches, I recognized 10 discrete types (Table 30) and tallied their frequency of occurrence (Tables 31 and 32). For general comparisons, I considered supplanting approaches as one of three categories: simple approaches (1-2), head nibbling approaches (3), and peck/jump approaches (4-7).

Comparisons of response pattern frequencies between populations or sex and age classes provide more meaningful information when stimuli are similar, that is, when motor patterns directed by supplanting condors are alike. Thus, I assembled the response frequencies according to the three general types of supplanting behavior. Although the 10 supplanting patterns are

Table 27. Catalogue of motor patterns directed by supplanting condors toward bird that is supplanted.

---

1 Approach by walking

2 Approach by landing

3 Head nibble

4 Pecking motion without contact

5 Peck with contact

6 Run or jump, sometimes with wings open

7 Run or jump, sometimes with wings open, and a pecking motion without contact

8 Run or jump, sometimes with wings open, and a peck

9 Multiple pecks, sometimes accompanied by contact with the feet, in an interaction 2 sec or less in duration

10 Multiple pecks, sometimes accompanied by contact with the feet, in an interaction more than 2 sec in duration

Table 28. Frequency of different supplanting motor patterns by condors feeding at the baits in the Colombia study area. Recorded from 1 October 1968 to 15 March 1969. Zero frequency for class combinations not listed.

Sex and age class of:		Total no. patterns recorded	Percent of Different supplanting motor patterns (Table 27)									
Supplanting Condor	Supplanted Condor		1	2	3	4	5	6	7	8	9	10
Adult male	adult male	8	62	0	0	0	0	12	0	12	0	12
	adult female	60	68	5	5	3	2	17	0	0	0	0
	immature male	38	55	16	0	0	8	18	0	3	0	0
	immature female	22	59	14	0	9	18	0	0	0	0	0
Adult female	adult female	4	75	25	0	0	0	0	0	0	0	0
	immature male	48	33	21	6	8	6	17	0	4	0	4
	immature female	5	80	20	0	0	0	0	0	0	0	0
Immature male	adult female	2	0	100	0	0	0	0	0	0	0	0
	immature male											
	a) unidentified	17	18	6	0	24	47	0	0	6	0	0
	b) IM2 supplants IM	81	41	0	0	37	19	0	1	2	0	0
	immature female	32	53	0	3	16	16	0	3	6	0	3

Table 29. Frequency of different supplanting motor patterns by condors feeding at a feeding area on Isla Zárate, Peru. Recorded from 8 October, 1969 to 22 February 1970. Zero frequency for class combinations not listed.

Sex and age class of:		Total no. patterns recorded	Percent of Different supplanting motor patterns (Table 27)									
Supplanting Condor	Supplanted Condor		1	2	3	4	5	6	7	8	9	10
Adult male	adult male	162	58	6	0	7	8	4	2	10	1	4
	adult female	399	58	4	2	9	7	7	6	8	1	0
	immature male	122	24	1	1	19	12	15	8	20	1	0
	immature female	20	65	0	0	0	10	5	5	15	0	0
	immature, sex unknown	9	33	0	0	0	22	0	11	33	0	0
Adult female	adult female	329	69	5	1	11	4	3	4	2	2	1
	immature male	44	34	0	0	23	27	7	0	0	5	5
	immature female	23	65	0	0	9	17	4	0	4	0	0
	immature, sex unknown	43	30	2	0	7	19	7	14	14	5	2
Immature male	adult female	27	81	0	0	11	4	4	0	0	0	0
	immature male	5	60	0	0	0	20	20	0	0	0	0
	immature female	11	91	0	0	0	9	0	0	0	0	0
		1194										

Table 30. Catalogue of response patterns by supplanted condors.

1	Move away immediately and continue to feed elsewhere
2	Head nibble
3	Motionless less than 5 sec in an erect posture followed by movement away to feed elsewhere
4	Remain motionless in an erect posture for less than 5 sec after moving away three steps or less
5	Remain motionless in an erect posture for less than 5 sec after moving away more than three steps
6	Remain motionless at the feeding site in an erect posture for 5 sec or more
7	Remain motionless in an erect posture for 5 sec or more after moving away three steps or less
8	Remain motinless in an erect posture for 5 sec or more after moving away more than three steps
9	Run from the feeding site
10	Peck back, sometimes accompanied by contact with the feet

Table 31. Frequency of different response patterns by condors supplanted from a feeding site. Recorded from 1 October 1968 to 15 March 1969 at baits in the Colombia study area. Zero frequency for supplanting patterns not listed.

Sex and age class of:		Type of supplanting motor pattern (Table 27)	Total no. patterns recorded	Percent of different response patterns by supplanted condors (See Table 30)									
Supplanting Condor	Supplanted Condor			1	2	3	4	5	6	7	8	9	10
Adult male:	adult male	1-2	5	80	0	0	0	0	0	0	20	0	0
		4-10	3	0	0	0	0	0	0	0	33	0	67
Adult female:	adult male	1-2	34	91	0	0	3	3	0	0	3	0	0
		3	3	0	100	0	0	0	0	0	0	0	0
		4-10	12	25	0	0	8	0	0	0	25	42	0
	adult female	1-2	4	100	0	0	0	0	0	0	0	0	0
	immature male	1-2	2	50	0	0	0	0	0	0	50	0	0
Immature male:	adult male	1-2	26	88	0	0	0	0	4	0	8	0	0
		4-10	9	33	0	0	0	0	0	0	22	44	0
	adult female	1-2	31	100	0	0	0	0	0	0	0	0	0
		4-10	7	0	0	0	0	0	0	0	43	14	43
	immature male (unidentified bird)	1-2	4	75	25	0	0	0	0	0	0	0	0
		4-10	13	38	0	0	0	0	31	0	0	0	31
	IM3 by IM2	1-2	23	100	0	0	0	0	0	0	0	0	0
		4-10	27	81	0	0	0	0	7	0	0	0	11
	immature female	4-10	1	0	0	0	0	0	0	0	0	0	100
Immature female:	adult male	1-2	16	100	0	0	0	0	0	0	0	0	0
		4-10	5	80	0	0	0	0	0	0	20	0	0
	adult female	1-2	5	100	0	0	0	0	0	0	0	0	0
	immature male	1-2	7	100	0	0	0	0	0	0	0	0	0
		3	1	0	100	0	0	0	0	0	0	0	0
		4-10	5	0	0	0	40	0	20	0	0	20	20

Table 32. Frequency of different response patterns by condors supplanted from a feeding site. Recorded from 8 October 1969 to 22 February 1970 on Isla Zárate, Peru. Zero frequency for supplanting patterns and class combinations not listed

Sex and age class of:		Type of supplanting motor pattern (Table 27)	Total no. patterns recorded	Percent of different response patterns by supplanted condors (See Table									
Supplanting Condor	Supplanted Condor			1	2	3	4	5	6	7	8	9	10
Adult male:	adult male	1-2	63	37	0	33	0	2	13	6	8	2	0
		4-10	38	0	0	8	5	8	3	11	29	8	29
Adult female:	adult male	1-2	91	42	0	19	2	0	9	10	18	1	0
		3	1	0	0	0	100	0	0	0	0	0	0
		4-10	81	4	0	9	9	4	5	20	30	17	4
	adult female	1-2	125	60	0	16	6	1	10	1	6	0	0
		3	3	0	67	33	0	0	0	0	0	0	0
		4-10	52	0	4	13	21	10	8	17	10	8	10
	immature	1-2	23	65	0	4	9	0	13	0	9	0	0
		4-10	6	17	0	0	0	17	33	0	17	0	17
Immature male:	adult male	1-2	21	52	0	10	1	1	33	1	5	0	0
		4-10	56	2	0	4	12	12	18	20	16	12	4
	adult female	1-2	5	20	0	0	0	0	20	20	10	0	0
		4-10	10	0	0	20	20	20	1	0	0	0	30
	immature	1-2	3	67	0	33	0	0	0	0	0	0	0
		4-10	2	50	0	0	0	0	50	0	0	0	0
Immature female:	adult male	1-2	4	100	0	0	0	0	0	0	0	0	0
		4-10	2	0	0	0	0	0	50	0	0	50	0
	adult female	1-2	2	50	0	50	0	0	0	0	0	0	0
	immature	1-2	5	80	0	0	0	0	20	0	0	0	0
			1	0	0	0	0	0	100	0	0	0	0
Immature (sex unknown)	adult male	1-2	1	0	0	0	0	100	0	0	0	0	0
		4-10	5	0	0	0	40	20	40	0	0	0	0
	adult female	1-2	4	0	0	25	0	25	0	0	50	0	0
		4-10	5	0	0	0	0	40	0	0	20	0	40

ranked roughly on a scale of action intensity, those of the response group, particularly the center responses (3-8), seem different only in a nominal sense, without reference to an ordinal ranking. To secure an index for evaluating population or class frequency differences for these responses I assembled data on all responses in a contingency matrix according to the simple and peck/jump type of supplanting pattern. The 10 recorded instances of head nibbling approach (3) were excluded from this treatment. I used a chi-square analysis to test each cell against the compressed matrix in search of positive or negative associations with the two approach types (Table 33).

A number of approach and response patterns were associated. In response to simple approaches, birds usually moved away and fed elsewhere within 5 seconds after being supplanted. With peck/jump approaches, the supplanted condors tended to move away from the carcass and stop feeding, at least briefly. All 41 peck-back responses followed peck/jump approaches. The patterns positively associated with peck/jump approaches (4,5, 7-10) are referred to as peck/jump-positive responses; those positively related to simple approaches (1,3) are called simple-positive responses. Response 6, remaining motionless in an erect posture at the feeding site for more than 5 seconds, seemed to occur independently of simple or peck/jump approach differences. Head nibbling also appeared to be independent, but the sample size of this response was quite small.

Comparison of Pattern Frequencies

I compared population and class differences in supplanting and response patterns with chi-square tests. A ten-column matrix was constructed for each comparison. I performed no tests when a single cell had an expected value of less than 0.5 or when 20 percent or more of the cells had expected values of less than 2.0. In these instances, matrices were reconstructed by combining column categories with the smallest frequencies until the preceding criteria were met.

Table 33. Frequency of different responses to simple and peck/jump approaches. Frequency for each type is tested against a compressed matrix. Chi-square values are listed and directions of association are noted for responses according to the peck/jump approach. Response patterns referred to as peck/jump-positive in the text are those positively associated with the peck/jump approach and those referred to as simple-positive (peck/jump negative) are positively related to the simple approach.

	Response pattern (see Table 30)										
	1	2	3	4	5	6	7	8	9	10	Total
Frequency of response patterns following simple approach (1-2)	313	2	63	14	5	41	15	41	2	0	496
Frequency of response patterns following peck/jump approach (4-10)	48	3	21	34	24	34	40	61	40	41	346
X^2 value	201.70	0.74	9.99	18.60	21.54	0.61	24.32	16.79	53.54	61.78	
Sign of association with peck/jump approach[a]	-	0	-	+	+	0	+	+	+	+	

[a] No association considered present (sign=0) when $X^2 < 3.84$.

Although 2 X 2 chi-square tests can often be used validly when expected frequency values are less than five, as recommended by Siegel (1956) (see Cochran, 1954), the effect of this revised criterion may affect the test's outcome when the degrees of freedom exceed one. The risk may be greater for rejecting a null hypothesis when it should be retained. Even though some of the probability values calculated with these revised criteria may be somewhat smaller than they ought to be, I was able to maintain a much higher resolution in search of discrete differences. In many cases, major departures in supplanting comparisons involved only those patterns that are relatively rare. Hence, the chi-square method used in these comparisons should be considered more as an index of association than as a test. Should the reader wish to perform tests using other criteria for minimum class samples he can obtain raw data for each comparison from Tables 28-32.

When differences are deemed significant, those categories with most deviant frequencies are discussed. Proceeding in this manner, I was able to detect and describe characteristic trends in data for different population, sex and age classes, and individuals, without recounting the basic distributions common to all. In approach comparisons, departures were evaluated according to a general pattern of differences toward simple or peck/jump types. Trends of departure in each response comparison are evaluated by considering response types with deviant frequencies as one of two general classes, peck/jump-positive and simple-positive (Table 33).

Rates of Supplanting

Interclass Comparisons. I searched for possible differences in the levels of supplanting activity across different sex and age classes for condors feeding on Isla Zárate by recording the frequency of these interactions per unit time. I figured the rate for across-class comparisons as the mean number of supplanting occurrences per 10 minutes of presence time by the supplanting class. For example, if adult males supplanted adult females three times in a 15-minute period

when two males and three females were present, I would compute condor minutes of the supplanting class as two males times 15 minutes, for 30 adult-male minutes or three 10-minute periods. So three supplanting occurrences would figure as a rate of 1.0 occurrences per 10 condor minutes of presence by the supplanting condor class, and this rate would be listed in Table 34 as a single occurrence in the 0.81-1.00 rate column for adult male-adult female classes, when there were more females than males. I designated each sample period as the time during which the individual composition of the birds on the ground remained constant. One period ended and another began whenever a bird arrived or departed. Most of the periods were 10 to 15 minutes in duration; the longest was 71 minutes. I excluded sampling periods of less than 5 minutes from the analysis. I compared different rate distributions by using chi-square tests according to the same guidelines established earlier for comparing supplanting patterns and responses (p. 126-127).

Effect of Group Size. I separated supplanting rates according to certain ratios for the number of condors present, not only to standardize interclass comparisons, but also to test for group size factors that might affect rates. If an individual of a supplanting class tended to move around a carcass at a given rate and also displaced members of a subordinate class as he went, the supplanting rate would increase with the number of subordinate class birds present. On the other hand, birds of the supplanting class might feed at acquired sites for durations independent of the number of subordinate class condors present. I found some evidence for the latter when I tested for differences in adult male-adult female supplanting rates in contexts where there were as many males as females and with those where females outnumbered males. Rate differences were not significant[1] to retain the null model that proposed increased numbers of subordinate adult females present had no effect on supplanting rate by adult males. Restricted sample sizes precluded similar comparisons for other classes.

Table 34. Rates of supplanting activity across and within different sex and age classes on Isla Zárate, Peru. Recorded from 8 October 1969 to 22 February 1970.

Ratio of potential interactants of different sex and age classes			Rate of supplanting activity: Percent of periods with following mean number of occurrences per 10 min of presence by supplanting birds											
Class supplanting		Class supplanted	0	0.01-0.20	0.21-0.40	0.41-0.60	0.61-0.80	0.81-1.00	1.01-1.20	1.21-1.40	1.41-1.60	1.61-1.80	1.81-2.00	>2.00	No. of observation periods
1 adult male	to	1 adult female	42	3	6	0	3	19	3	3	3	3	0	17	36
1 adult male	to>	1 adult female	31	3	5	5	10	10	4	6	0	4	5	16	77
1 adult male	to	1 immature	61	3	3	9	0	6	3	0	0	3	6	6	33
1 adult male	to>	1 immature	67	0	0	0	33	0	0	0	0	0	0	0	3
1 adult female	to	1 immature	78	6	0	0	0	6	3	0	0	0	0	6	32
1 adult female	to>	1 immature	100	0	0	0	0	0	0	0	0	0	0	0	2
1 adult female	to	1 immature male	88	0	0	0	0	0	0	0	0	0	0	12	16
1 immature male	to	1 adult female	56	0	0	12	0	6	6	0	6	6	6	0	16
Number of potential interactants for within-class comparison			Percent of periods with mean number of supplanting occurrences listed above per 5 min of presence by condors of one class											
2 birds:														
adult male			72	0	0	2	0	2	0	0	0	5	8	10	40
adult female			59	0	2	4	0	4	2	4	2	10	0	12	49
> 2 birds:														
adult male			40	5	11	11	4	11	0	9	0	2	2	7	57
adult female			38	2	9	8	13	5	2	1	2	1	4	14	85

Intraclass Comparisons. To make rate comparisons within class, I recorded supplanting class minutes as the total number of condor minutes for the class considered and assumed that no within-class hierarchy existed (Table 34); in the absence of such a hierarchy, two birds of the same class could supplant each other. For this reason, I calculated rates on the basis of 5 minutes of presence instead of the 10-minute segment used in interclass categories, where supplanting behavior was usually unidirectional. As these data will show later, the assumption of no dominance in intraclass interactions appears unfounded.

Aerial Pursuits

Five sets of observational data indicate that, despite an implication of intent, the term "pursuit" may be more appropriate than a mere physical description for this particular type of aerial interaction: (1) The flight of the lead condor appears evasive relative to that of the bird following. The lead bird flaps more and does not lower his feet, a typical braking movement. Turns of the lead bird are sharp, occurring an instant before those of the following bird. (2) The condor following sometimes strikes the lead bird. (3) When supplanting activity extended on into an aerial chase from the feeding area, the supplanted condor always led (Plate 23). (4) In 84 pursuits by two class-identified condors, the lead bird belonged either to the same sex and age class of the bird following or to a class considered subordinate (Table 35). (5) I saw each member of a nesting pair involved in this aerial interaction with other condors but never with each other. Data on aerial pursuits presented in Table 35 are discussed in the section of this chapter dealing with relations in the air and on the perch. Flight patterns typical of the aerial pursuit are described in Chapter 8.

Nibbling and Preening

Table 35a. Frequency of aerial pursuits observed in Peru and Colombia from 18 June 1968 to 15 May 1970.

Bird pursuing ->	Frequency of occurrence[a]				
	Adult male				Adult female
Bird pursued ->	Adult		Immature		Adult female
	Male	Female	Male	Female	
Entire pursuit in air:					
a) Colombia study area	1	5	1	2	2
b) Paracas area, Peru	9	6	2	0	0
c) Other Peru areas	2	1	0	0	1
Lead bird chased from the ground at least once:					
A) In feeding area					
1) Pursuit continues in air after lead bird departs					
a) Colombia study area	3	17	1	0	1
b) Paracas area, Peru	2	0	0	0	0
2) Running pursuit on ground, lead bird departs, other remains					
a) Colombia study area	0	11	1	0	1
b) Paracas area, Peru	1	3	0	0	1
B) In cliffside roost and perch areas, both birds fly					
a) Colombia study area	1	1	1	1	1
b) Paracas area, Peru	1	0	1	0	3
Total	19	43	6	2	9

[a] Zero frequency observed for class combinations not listed. An extended pursuit interrupted by pauses of less than 15 min in duration considered as one occurrence. Interactions involving more than two condors not included.

Table 35b. Frequency of aerial pursuits observed in Peru and Colombia from 18 June 1968 to 15 May 1970.

Bird pursuing ->	Frequency of occurrence[a]				
	Adult female		Immature male		
Bird pursued ->	Immature		Immature		
	Male	Female	Male	Others[b]	Total
Entire pursuit in air:					
a) Colombia study area	0	0	1	78	90
b) Paracas area, Peru	0	0	0	9	26
c) Other Peru areas	0	0	0	1	5
Lead bird chased from the ground at least once:					
A) In feeding area					
1) Pursuit continues in air after lead bird departs					
a) Colombia study area	0	0	0	11	33
b) Paracas area, Peru	0	0	0	0	2
2) Running pursuit on ground, lead bird departs, other remains					
a) Colombia study area	1	3	0	1	18
b) Paracas area, Peru	0	0	0	0	5
B) In cliffside roost and perch areas, both birds fly					
a) Colombia study area	0	0	0	10	10
b) Paracas area, Peru	0	0	0	1	6
Total	1	3	1	111	195

[a] Zero frequency observed for class combinations not listed. An extended pursuit interrupted by pauses of less than 15 min in duration considered as one occurrence. Interactions involving more than two condors not included.

[b] Sex of one of both members unknown.

Table 35c. Frequency of aerial pursuits observed in Peru and Colombia from 18 June 1968 to 15 May 1970.

	Frequency of occurrence[a]			
Bird pursuing ->	Adult	Adult	Immature	
Bird pursued ->	Adult	Immature	Immature	Total
Entire pursuit in air:				
a) Colombia study area	39	49	2	90
b) Paracas area, Peru	19	5	2	26
c) Other Peru areas	5	0	0	5
Lead bird chased from the ground at least once:				
A) In feeding area				
1) Pursuit continues in air after lead bird departs				
a) Colombia study area	29	3	1	33
b) Paracas area, Peru	2	0	0	2
2) Running pursuit on ground, lead bird departs, other remains				
a) Colombia study area	13	2	3	18
b) Paracas area, Peru	5	0	0	5
B) In cliffside roost and perch areas, both birds fly				
a) Colombia study area	3	7	0	10
b) Paracas area, Peru	5	1	0	6
Total	120	67	8	195

[a] Zero frequency observed for class combinations not listed. An extended pursuit interrupted by pauses of less than 15 min in duration considered as one occurrence. Interactions involving more than two condors not included.

Plate 23. An adult male chasing another adult from the bait in Colombia study area.

Description

One pattern of interaction frequently observed among condors was the manipulation of skin or feathers on one bird by the beak of another (Plate 24). When nibbling involved the head and neck region, it was usually a mutual activity, but when feathers were manipulated, the preened bird often stood quietly without any apparent response.

Social nibbling often occurred during protracted interactions in which aggressive motor patterns (as in peck/jump approaches) were notably absent. I saw nibbling activity during interactions between parent and nestling and, at times, in precopulatory interactions between members of an adult pair. Koford (1953, pp. 95-96) noted instances of mutual head and neck nibbling by a nesting pair of California condors. Bouts of nibbling observed at the baits for both black and turkey vultures were rare and brief.

Variation Among Different Populations

Varying levels of individual recognition may account for general nibbling pattern differences noted among Andean condor populations. In the Colombia study area and in the Cerro Illescas of Peru, we saw condors nibble each other longer and more often than those on Isla Zárate. The individual composition of the first two populations probably changed much less in a given period of time than it did on the Peruvian coast near Isla Zárate, so individuals may have recognized one another better than they did on the island.

Component movements in the nibbling patterns in the first two areas seemed slower and smoother than those between members of the transient Zárate populations. Entire patterns observed in Colombia and northern Peru usually were more complex; sometimes they involved three birds. In the Cerro Illescas, I watched one trio of males engage in nibbling activity for several minutes; in Colombia, I saw three stage-1 immature males (IM1, IM2, and IM3) meet at one feeding point on the bait and nibble at each other's heads simultaneously. On another

Plate 24. An adult male and female engaged in mutual head nibbling at a bait in the Cerro Illescas

occasion at the Colombia bait I saw three birds, AM3, IM3 and an adult female, interact alternately in pairs. At a bait in the Cerro Illescas, I saw four different pairs of condors engaged in head nibbling activity at once. Most of the interactions lasted several minutes. I saw no aggressive patterns in any of the activities.

Origin of the Pattern

The presence of long, slow moving nibbling patterns appeared to be negatively associated with the presence of aggressive or peck/jump patterns. In contrast, short, rapid nibbling patterns seemed characteristic of aggressive encounters. Sometimes rapid nibbling encounters developed into contested fights. Peck/jump supplanting interactions often involved mutual beak and head nibbling.

In one typical encounter an adult female feeding with her head inside a carcass apparently did not see the approach of an adult male. He bit her on the wing. She pulled her head out immediately, they touched beaks, and she withdrew. Once at the Colombian bait, IM3 stood near IM1 when the latter bit at a black vulture. When IM1 snapped his head to an erect position, he nearly bumped the head of IM3. Instantly, they nibbled heads and beaks quickly for a moment before separating.

Movements in social nibbling patterns resemble those of pecking and parrying patterns in peck/jump encounters and may have developed from them. When one condor supplants another with a peck, the supplanted bird often extends his head toward the other's head and follows its movement while slowly backing away. Such a maneuver probably wards off other pecking blows to parts of the body that are vulnerable when undefended by a beak. If the supplanting bird males another pecking motion, his beak is met by the beak of the subordinate bird in an apparent parrying motion. Frequently, then the dominant bird makes a series of short, jabbing, peck motions. When each motion is parried, the interaction resembles a normal head-nibbling

pattern, with the rate of movement accelerated.

In a protracted nibbling interaction observed in the Cerro Illescas between an adult and sub-adult male, the slow movements by each bird in manipulating skin on the side of each other's head appeared also to prevent or thwart the other bird from nibbling back. For example, at one point, the side of each bird's head was pressed against the other's, with the beaks facing in opposite directions. Male #1 was manipulating skin on the side of #2's head near the occiput. Male #2 turned his head toward #1; because the head is longer than it is wide, the beak acted as a kind of lever that pushed #2 away from the area he was nibbling. Then #2 nibbled at the side of #1's head, and #1 prevented him similarly. This bout lasted several minutes without any pecking or other abrupt movements. The peck-and-parry pattern and the protracted, slow-moving nibbling patterns seem to be related, along a continuum, by intermediate patterns.

Function

I looked for general frequency differences for the protracted pattern in different setting in search of clues to function. I found that IM3 initiated all six nibbling interactions observed with IM2; encounters after one of the birds had just landed were excluded. According to the direction of supplanting activity, IM2 dominated IM3. Initiated by the vulnerable subordinate bird, the pattern may help thwart peck/jump encounters. Yet when I examined interclass nibbling interactions, I could find no consistent pattern by embers of either the subordinate or dominant class in initiating the bouts. I did not, however, an infrequence of social nibbling when the participants were both females. I saw only one interaction between immature females; I recorded no instances when an adult female approached either an immature female or another adult female. Adult females avoided each other at the Colombia baits (Figure 24); this might explain, in part, the dearth of social nibbling between females. The tendency by adult males toward social nibbling could be related to male-specific aggressiveness. Such aggressiveness

may be important in competing for nest areas or mates and might not be advantageous at feeding areas, where social behavior seems to facilitate use of a large and temporary food supply by many birds. In this case, one would expect selective pressure for a behavioral mechanism that acted to suppress overt aggression. Social nibbling might be such a mechanism.

Lead-Follow Relations

I examined one aspect of activity coordination for two adult pairs in Colombia by recording which bird took off or landed first within 10 m of the other when the other member followed within 5 minutes. In landing, the female followed the male in 20 instances for pair 1 and 17 for pair 2. Similar frequencies for males following females were 17 and 15. For both pairs, there was no significant trend by either male or female to land first. In taking off, however, the male of pair 1, a non-nesting pair, flew first more often, whereas for pair 2 the female did so. The female followed the male 27 times for pair 1 and 10 times for pair 2, whereas males followed in only 15 instances for pair 1 and 31 instances for pair 2, a significant difference.[2] I noted also that AM2 tended to follow AF2 when they flew in the area of the nest. Such differences may have been specific either to the individuals or to the nesting status. Unlike her mate or the mates of the non-nesting pair, the nesting female was never observed in any courtship postures. This tendency toward "independence," where she departed first and led in nest area flight paths, might have been a reflection of a more dormant sexual state. Koford (1953, p. 96) noted that one nesting California condor usually followed its mate in walking and taking off; *Gymnogyps* is not sexually dimorphic, so he was unable to determine sex of either mate.

Landing or taking off by one member of a pair may have induced the other to do the same. Plotting logarithms for the cumulative frequency of intervals separating occurrences of

landing or take off by both members of pairs 1 and 2 against interval duration indicates that the probability of one bird following another is greatest during the first 15-second interval, particular for landing (Figure 25, see also p. 80).

RELATIONS AT FOOD

Adult Males and Adult Males

Associations

In general, adult males avoided each other. When they did meet, interactions were comparatively aggressive. In Colombia, adult males rarely visited the bait at the same time. A second adult male arrived less often than expected when one adult male was already present, either alone or as a member of a group (Figure 24). This negative association for arrival probably explains, at least in part, the absence of adult males remaining after an adult male departed.

Although adult males arrived and departed more often when other condors were present, they commenced and ceased feeding more frequently when no others fed, especially males (Figure 24). Adult males were alone at the bait only about one quarter of their total visitation time, yet they fed alone more than half of the feeding time (Table 25). Usually other condors stopped feeding and moved away from the carcass when an adult male began to feed. As a dominant class, adult males could arrive with priority of access to the food after the presence of others had demonstrated the safety of landing at the feeding site. This explanation may also apply for within class trends. Of the four identified adult males in Colombia, only AM1 tended to arrive less frequently when no other condors were present (Figure 26), and AM1 was the dominant male. I saw him supplant both AM2 and AM3. During the extent of this study, all

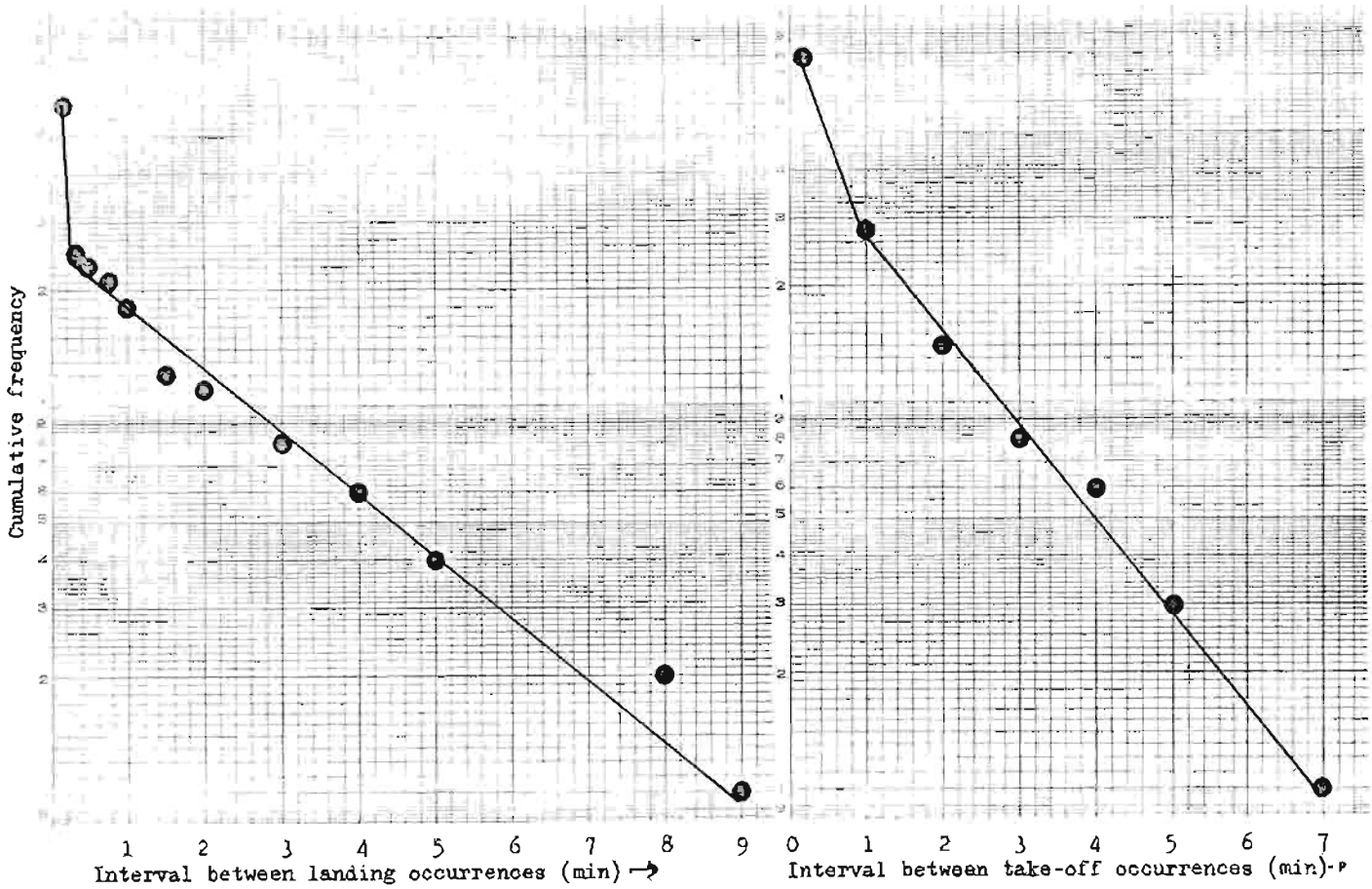

Cumulative frequency
1 2 3 4 5 6 7 8 9
Interval between landing occurrences (min) →
0 1 2 3 4 5 6 7
Interval between take-off occurrences (min)

Figure 25. Lgarithms for the cumulative frequency of intervals separating occurrences of take-off or landing by two members of an adult pair plotted against interval duration. Data recorded for pairs 1 and 2 when pair members landed or took off from perches <10m apart (n=78, 60). Separate graphs constructed for the four individual condors were similar to each other in both comparisons, so the data were combined.

Already present	Arriving: AM1	AM2	AM3	AM4	Other Condors	
No condors	6.45 – 1	0.65 9	0.19 7	0.15 7	140	164
One or more condors	16	12	16	11	254	309
	17	21	23	18	394	473

Figure 26. Distribution of arrival frequencies at the bait in Colombia for four identified adult males according to the presence or absence of other condors. Treatment same as in Figure 24.

supplanting by identified condors was unidirectional; I saw no exceptions.

Fighting

Adult male participated in fights more often than other condors. Although sample sizes are small and differences are not statistically reliable, the data in Table 26 suggest that, relative to females and immature birds, adult males engaged more often in intraclass fights and less often in interclass fights. I observed 1.82 adult male intraclass fights per condor hour when two or more intraclass condors were present, compared to a similarly derived value of 0.08, the highest value for intraclass fights for members of other sex and age classes. On the other hand, none of eight interclass fights recorded between two birds involved adult males. Interclass fights with adult males are rare, no doubt, because birds of other classes avoid them.

As to the relatively large number of male intraclass fights, one of two conditions may exist: Relative to other classes, adult males tend to attack more often and/or more actively than either (1) any individual or more specifically, (2) any adult male. In search of additional information on the stimuli to which the male responded, I compared intraclass supplanting rates between adult males and females (Table 34) and found that differences were not significant.[3] That males do not seem to supplant each other at a higher rate than do females supplant females provides some evidence that, regardless of the sex and age class of the other individual, adult males tend to fight with any individual contesting an attack.

Supplanting

In supplanting encounters, adult males again were characteristically aggressive with each other. In three general comparisons, I found that they pecked at each other more often than other birds did: (1) The type of supplanting approach by adult males on Isla Zárate varied according to the class they supplanted, considering three classes -- adult males, adult females, and immature birds.[4] The largest deviation in adult male-adult male encounters was the high frequency of

multiple peck attacks (pattern 10); run or jump patterns occurred less often than expected. (2) Responses by adult males, adult females, and immature birds on the island differed significantly to both simple approaches by adult males[5] and peck/jump approaches.[6] For the latter approach category, the most notable departure in adult male response categories was a high frequency of peck back responses (pattern 10), whereas in the simple approach the greatest departure was a positive one for the move-away-and-feed-elsewhere response (pattern 3). (3) In intraclass supplanting interactions, adult males responded to peck/jump approaches with peck/jump positive responses more often than adult females did. Response differences were significant for both peck/jump approaches[7] and simple approaches,[8] but in the latter case, the trend of the departures was not consistent according to a dichotomy between simple-positive and peck/jump-positive responses. In the peck/jump approaches, adult males responded to adult males by (a) a cessation of feeding and movement away (pattern 5) and (b) pecking back (pattern 10) proportionally more often than adult females did to other adult females. In similar comparisons with approach and response data from Colombia, differences were not reliable; sample sizes were smaller for that area.

Adult Males and Adult Females

Associations

Relationships between adult males and females were characterized by (1) positive associations and (2) clear dominant-subordinate positions. At the Colombian baits adult males arrived more often than expected by chance alone when an adult female was present (Figure 24). Although the deviation was not substantial[9], adult females seemed attracted to the bait by the presence of an adult male. Similar positive relations existed for departure partly, perhaps partly as a consequence of the arrival associations. The large number of departures by an adult female

when an adult male remained probably reflects, in part, a number of adult male chases in which the pursued female flew. At the bait itself adult females commenced and ceased feeding more often than is attributable to chance when an adult male was already feeding. Females frequently walked away from the bait when males landed and waited until the male began feeding before feeding again themselves; when supplanted by males they often stopped feeding entirely and either flew or waited until the male left the bait before feeding again. Although it is probable that many of the adult males and adult females feeding together in Colombia were pairs that also foraged, roosted, and nested together, some pairs observed together may have been unrelated for the most part in their daily activities. Once an adult female fed with AM3; when he flew, another adult male landed and she fed at the bait with him.

Supplanting

Adult males were clearly dominant over adult females. I saw 459 supplanting incidents between adult males and females, and not once did the female supplant the male. As noted earlier, less aggressive patterns seemed to be employed more often by adult males on Isla Zárate when adult males, rather than adult males, were supplanted. This may have depended partly on differences in response by the supplanted bird. For example, the most substantial deviation, a comparatively low frequency of a multiple peck pattern (supplanting pattern 10) when females were displaced, may have been due to a more active avoidance response by the females.

Evidence for this interpretation exists in two comparisons of supplanting responses: (1) With data from Isla Zárate I examined the significant variation in adult female responses to the simple supplanting approach of adult males, adult females, and immature birds[10] and to the peck/jump supplanting approach of adult females and adult males[11]; for both general types of approach the major departures for responses characterizing adult male-adult female interactions was a relatively large number of occurrences for pattern 8, a withdrawal response. (2) Response

patterns by adult females, adult males, and immature birds on Isla Zárate differed significantly to both simple and peck/jump approaches by adult males (p. 136). For simple approaches, the most notable departure in adult female responses again was a positive deviation for pattern 8, the withdrawal response. In peck/jump approaches, adult females tended to make simple positive responses with a negative deviation for pattern 10, a peck-back response, and a positive one for pattern 6, in which the bird assumed an erect posture.

Adult male-adult female supplanting encounters tended to be less aggressive in Colombia than on Isla Zárate, a general trend for all supplanting activity. Males in Colombia supplanted females proportionately more often by running or jumping with wings open (pattern 6) than did condors in Peru, whereas the Peruvian males supplanted females more often in running or jumping patterns associated with a pecking motion (patterns 7, 8). Differences in the pattern frequencies were significant.[12] In simple supplanting approaches by adult males, Colombian females moved away and fed elsewhere (pattern 1, a simple positive response) proportionately more often than females on the island; differences again were significant.[13]

Data from individual observations on adult male-adult female relations at the feeding area were varied, with no consistent trends were apparent. Sometimes an adult male and female arrived, fed, and left together, and sometimes a male chased a female from the feeding area, either upon the first encounter or, occasionally, after feeding with her for a short period. Courtship and copulations patterns occurred at feeding locations as well.

Adult Males and Immature Condors

Male Associations

Two basic relationships characterized adult male-immature male relations at the feeding area: (1) Adult males were clearly dominant over immature males, and (2) the two age classes

were negatively associated. Adult males did not arrive at the bait in Colombia as often as expected by chance when an immature male was present (Figure 24). In view of the dominance relations between the two age classes, it seems unlikely that adult males actively avoided immature males. Adults may arrive at a feeding site only under optimum conditions, whereas younger birds, without priority of access, may be forced to tolerate more marginal conditions. Such an age-related factor could be responsible for a negative association.

Adult males commenced and ceased feeding more often than expected during periods when immature males were not feeding (Figure 24). When an adult male landed and walked toward the bait, immature males that were feeding usually walked away before he reached it. Many times the immature birds did not feed until the adult left; sometimes they flew after watching him for several minutes. They tended to depart from the bait more often than expected when an adult male was present. In some cases, they were actively chased away.

Male Supplanting Activity

The dominance of adult males over younger males was clearly expressed; in all of the 160 encounters recorded between males of the two age classes, adult supplanted immature condors. In supplanting immature males, adult male tended to be comparatively aggressive. On Isla Zárate, adult male supplanted immature males with peck/jump approaches (particularly patterns 4-8, Table 27) proportionately more often than they did when displacing other adults; differences were significant.[14]

In general, young males did not peck back or contest supplanting approaches by adult males. I tested for differences in the frequency distribution of immature male response patterns according to (1) simple approaches by adult males, adult females, and immature males in Colombia, (2) simple approaches by adult males and adult females on Isla Zárate, (3) peck/jump approaches by adult males, adult females, and immature males in Colombia, and (4) peck/jump

approaches by adult males and adult females on Isla Zárate. Of the four tests, the distributions in one comparison (#3) differed significantly.[15] The absence of pattern 10, a peck-back response, was the most notable deviation in the distribution of frequencies for immature male response patterns to adult male peck/jump approaches.

Population Comparisons

Adult male-immature male relations were less aggressive in Colombia than on Isla Zárate. The frequency recorded for simple approaches in Colombia, relative to the island, was large, whereas that of peck/jump approaches (patterns 4, 7, and 8 in particular -- Table 27) was small. Differences were significant.[16] As discussed in more detail in the section on the functions of dominance, differences in the response of immature males between the two study areas included the response of immature male between the two study areas included positive deviations for the "hesitation response" (pattern 6) by the Peruvian birds to both peck/jump and simple approaches by adult males. In addition, immature males on the island seemed more active in avoiding a second encounter with the supplanting adult. Young males on the island continued feeding elsewhere (pattern 1-Table 27) proportionately less often than Colombian birds and moved away from the bait (pattern 7) more often. This trend may have resulted, in part, to the differences in the array and configuration of food; on the island at this time, carcasses were smaller and more plentiful.

Adult Male-Immature Female Relations

Immature females were subordinate to adult males at the feeding area, but unlike condors of other sex and age classes, young females did not actively avoid adult males and, at times, even appeared to pester them when they fed. On several occasions, I saw immature females persist at feeding in the same holes with adult males, even after the males pecked at them.

On Isla Zárate, adult male supplanting approaches directed toward immature females

were less aggressive than those directed toward immature males.[17] The frequency of the simple walking approach (pattern 1) was comparatively greater, whereas a pecking approach (pattern 4) was less frequent. I detected no such differences among the birds at the Colombia site. Differences in supplanting approach patterns between the two study areas were not reliable, nor were there any characteristic trends in the response data for supplanting interactions between adult males and immature females. The sample sizes for the latter, however, were small.

Adult Females and Adult Females

Typically, adult female-adult female encounters were less aggressive than encounters that involved males, yet adult females still avoided each other. They did not arrive at the Colombian bait as often as expected by chance when another was present, nor did they feed as frequently as expected when another was feeding, either as a lone bird or as a member of a group (Figure 24).

Supplanting Activity

Approach. Supplanting approaches among adult females on Isla Zárate differed significantly[18] from those recorded among adult males, being less aggressive. Two peck/jump approaches (patterns 8 and 10) were used relatively less often by adult females supplanting one another. On the island, supplanting approach patterns by adult females toward adult females were less aggressive than those directed by adult males toward adult females.[19] When one female supplanted another, two peck/jump approaches (patterns 6 and 8, Table 27) occurred less often than expected. When I compared adult female supplanting approach patterns directed toward adult females with those directed toward immature males (see the section on the function of dominance), I found once more that adult female approaches were less aggressive in intraclass interactions. I recorded only four occurrences of supplanting activity between adult females in Colombia, so I was unable to make any meaningful comparisons with quantitative data from that

population.

Response. In several comparisons, response patterns for adult female-adult female supplanting encounters tended to be of the simple positive types, another indication of characteristic nonaggressiveness. Adult female responses differed according to the class supplanting both for simple approaches by adult males, adult females, and immature birds[20] and for peck/jump approaches by adult males and adult females.[21] In the first comparison, a peck/jump positive response (pattern 8) by females occurred less often than expected and a simple positive response (pattern1) more often. I found no consistent pattern in deviations toward simple positive or peck/jump positive response patterns in the second comparison, nor did I find a consistent pattern in deviations when I compared response patterns for intraclass supplanting interactions of adult females with those of adult males.[22] When I pooled these intraclass response data into two general categories, peck/jump positive and others, and then tested, I did find a possible difference in peck/jump approaches ($p < 0.10$)[23]: Adult males tended toward peck/jump positive responses more often than adult females.

We were unable to identify individual adult females because we could not find any distinguishing characters. If individual recognition figures in the supplanting relationships of adult females, one observation suggests a high level of discrimination. An adult female landed near a feeding adult female and ran at her with wings flapping. The feeding bird, head deep inside the carcass, was bitten and held by the neck, but after a brief struggle pulled loose, ran 2 m away, and stood motionless in an erect posture while the newcomer fed. If the second condor recognized the first as an individual, she did so either (1) by identifying cues of the bird on the ground while she was in flight or (2) by identifying cues from the body alone after she landed.

Adult Females and Immature Condors

Supplanting Activity

Adult females and immature males did not supplant each other in any consistent direction; observations indicate that dominance relations between the two reverse as the young males mature. In general, younger immature males were subordinate to the adult females, whereas sub-adult males were dominant. Once I saw four adult females together watch a sub-adult male feed alone on a sea lion pup.

Supplanting interactions between adult females and immature males were relatively aggressive, particularly so when the females supplanted males. A typical supplanting interaction by an adult female toward an immature male began when the female approached with lowered neck and head and directed an open beak toward the anterior part of the male. Usually, the male turned his head toward hers, opened his beak, and backed away from the feeding point while following the position of her head with his.

I searched for supplanting characteristics specific to this interclass relation by comparing pattern distributions for adult females displacing immature males with those of adult females displacing adult females. On Isla Zárate, adult females supplanted members of the two classes differently[24], generally using more peck/jump patterns to supplant adult females; those used for immature males involved pecking motions (patterns 4 and 5) more often and simple walking approaches (pattern 1) less. Differences were not significant in a similar comparison with Colombian data but the sample size was small. I did find in Colombia that immature males responded to the peck/jump approach of an adult female with peck/jump-positive responses more often than they did when peck/jump approaches were employed by either adult males or other immature males.[25] In addition, the young males in Colombia clearly responded to peck/jump and simple approaches by adult females according to the dichotomy of patterns displayed in Table

33, peck/jump-positive and simple-positive.[26] In a similar comparison with Peruvian data, however, differences were not reliable.

A Comparison of Antipodal Contexts. I saw adult females on the island supplant immature males 44 times; the reverse occurred 27 times. Unfortunately, I was unable to distinguish different age classes of the immature birds. I compared approach and response characteristics and supplanting rates for the two antipodal contexts and found three particular relations of interest: (1) Supplanting approaches by adult females toward immature males were more aggressive than those of the younger males toward the females. Relative to adult females, immature males used a simple approach (pattern 1) more often and a pecking approach (pattern 5) less often.[27] (2) To simple approaches, immature males responded in peck/jump positive patterns relatively more often than adult females.[28] I could not make similar comparisons for (a) peck/jump approaches on the island and for (b) both approach types in the Colombian area, because sample sizes were too small. (3) Immature males supplanted adult females more frequently than adult females supplanted immature males per unit of time. Rates recorded on Isla Zárate, during periods when the number of immature males equaled that of the adult females, differed significantly, with immature males supplanting adult females more often than the reverse for given periods of time.[29] Aside from noting the general aggressiveness that characterizes female-supplant-male interactions it is difficult to generalize, largely because it is impossible to attribute interclass characteristics in supplanting patterns and responses to intrinsic differences belonging to either one class or the other. This problem is discussed in more detail in the section on dominance structure.

Male-Female Fights

I observed a total of eight interclass fights in all areas, five of which were adult female-immature male quarrels. Two fights in Colombia involving IM2 were brief. For only a few

seconds each bird jumped, pecked at, and bit the other's head. Then, in each instance, the female fed after a short pause, and IM2 watched. On Isla Zárate, one fight between an adult female and a stage-2-immature male ended with the male feeding and the female standing nearby and watching. In another quarrel on the island between an adult female and a stage-2-immature male, the female fed and the male left.

Immature Female Relations

Although I secured little data on relations between females of different age classes the few interactions I did observe resembled those noted between immature females and adult males: Young females were subordinate to older ones, but they did not seem to actively avoid the pecking blows of peck/jump supplanting approaches by the dominant female.

At a bait on the coast near Paracas I watched four female condors interact once for 30 minutes; the four appeared to be of different ages. Differences in plumage and eye color seemed to provide a fairly reliable rank order of age (see p. 24-25 for a description of these birds). The expression of dominance, as defined by the direction of supplanting activity, among the four was linear, with the rank order of dominance matching the proposed rank order of age. The adult (#1) supplanted each of the other three birds at least once. Sub-adult #2 displaced females #3 and #4, and sub-adult #3 supplanted immature condor #4. There were no reversals. This relation was in contrast to that observed for three immature males in Colombia, where the proposed rank order of age was not directly related to the rank order of dominance.

Immature Condors and Immature Condors

Male Associations

In Colombia, immature males were attracted to each other. Relative to other classes, they spent a greater proportion of time on the ground and feeding in the company of another condor

(Table 25). Members of other classes visited the baits alone 24 to 30 percent of the time whereas immature males were alone only 17 percent of the visitation time. Usually, the associated birds were other immature males; young males were more likely to arrive when another was already present (Figure 24). In particular, both IM2 and IM3 landed more often than expected after one of them had already arrived (Figure 27). I was unable to determine whether similar associations occurred in Peru because I seldom saw immature males there.

Despite this attraction, immature males in Colombia did avoid landing when there was more than one condor already on the ground; they left the bait area more often either (1) when no other condors were present or (2) when one immature male remained (Figure 24). The first condition may be related to class differences in visitation durations. Typically, immature birds remained at the baits longer than adults; the mean value for 155 visitation durations by immature males was 22.1 minutes, compared to 6.4 and 8.8 minutes for 167 and 145 durations by adult males and females (Table 25).

Data on the contexts of departure for IM2 and IM3 also illustrate the relationship (Figure 27). IM2 left more often when IM3 remained, and IM3 departed more often when no other condors were present. The differences reflect the longer visitations of IM3 when the two fed together (Table 25).[30] In the context of feeding as well, immature males appeared to prefer the presence of other immature males (Figure 24 for all classes, Figure 27 for IM2 and IM3). They avoided feeding alone; neither IM1 or IM2 commenced feeding as frequently as expected when no other condors fed. Immature California condors also display a greater attachment to each other than they do to adults (Koford, 1953, p. 32).

Male Supplanting

Despite their positive associations, immature male Andean condors were relatively aggressive in their encounters with each other. Differences were reliable in the proportion of

Arriving / Present	IM1	IM2	IM3	Other Condors	
no condors	2.20 2	3.96 − 11	1.85 17	134	164
IM1		0	1	2	3
IM2	0		16.75 + 5	8	13
IM3	1.13 0	90.57 + 21		16	37
Others alone or groups	11	18	15	212	256
	13	50	38	372	473

Departing / Present	IM1	IM2	IM3	Other Condors	
no condors	0.41 4	1.17 10	23.59 + 23	108	145
IM1		0	1	3	4
IM2	0		3	8	11
IM3	2	59.84 + 16		19	37
Others alone or groups	2	7	1	164	174
	8	33	28	302	371

Figure 27a. Associations of three identified immature males at the Colombian baits as described by the frequencies of four differemt events. Treatments same as in Figure 24.

Commence feeding / Already feeding	IM1	IM2	IM3	Other Condors	
no condors	12.94 – 1	4.84 – 25	0.54 29	173	228
IM1		0	1	0	1
IM2	1		37.06 + 10	4	15
IM3	2	58.13 + 17		8	27
Others alone or groups	6	8	9	63	86
	10	50	49	248	357

Stop feeding / Feeding	IM1	IM2	IM3	Other condors	
no condors	2.88 3	1.43 26	1.55 24	163	216
IM1		0	3	0	3
IM2	0		20.94 + 8	8	16
IM3	0	24.42 + 11		12	23
Others alone or groups	5	8	7	51	71
	8	45	42	234	329

Figure 27b. A continuation of Figure 27a.

simple and peck/jump approaches for immature male, adult male, and adult female within-class supplanting encounters in Colombia.[31] Of the 98 immature male approaches, 81 were by IM2 toward IM3; differences in the proportion of the two approach types between these two young males and the remaining 17 instances for other young males were not significant nor were differences between adult male and immature male distributions. Supplanting approaches by males toward males were of the peck/jump type more often than expected. Like adult males, immature males (particular IM2 in this comparison) behaved more aggressively than adult females in the supplanting approach. The most obvious difference in intraclass relations between adult and immature males at the feeding area was the negative association of adult males, in contrast to the positive one for immature males.

Relations Among Three Particular Birds

Correlates of dominance. Supplanting interactions among the three identifiable immature males clearly demonstrated the presence of a linear intraclass hierarchy at the feeding area, with IM1 dominant over IM2 and IM3, and IM2 over IM3. I saw IM1 supplant IM2 and IM3 seven times each and IM2 supplant IM3 81 times. No supplanting in reverse contexts was seen. Several characteristics of the three are interesting correlates of supplanting behavior. Gradations of size and wariness had the same ordinal positions among the three as dominance, with IM1 the largest and most wary. However, IM1 also may have been the youngest for he had more down feathers on his neck than the others. He seemed more cautious than the other two and ran from the bait, sometimes flying, more frequently than the other immature birds in apparent response to the sound disturbances by black vultures. He looked up and around more often while feeding. Once when an adult female landed above the bait where the three young males fed, only IM1 stopped feeding and walked away from the bait. IM2 was smaller than IM1 but larger than IM3. His neck had less down and was redder in color than that of the others, which suggested he was

older. IM3, smallest of the three, seemed the least responsive to disturbances. I never saw him supplant any other immature males. Although these three immature males frequently visited the baits together, IM2 and IM3, in particular, rarely visited it one without the other. I saw this pair foraging and roosting together as well.

Variation in the Tempo of Social Activity. At the bait, IM2 and IM3 interacted with each other more frequently in a given unit of time than they did with other immature males, specifically IM1. IM3 was supplanted by IM2 more often in a given period than either IM2 or IM3 were by IM1. IM1 and IM2 were observed together 1.4 hours, providing a mean value of 5.0 supplanting occurrences per hour of joint feeding time. For IM1 and IM3, joint feeding time at the bait was 1.7 hours and the rate of supplanting was 4.1 occurrences per hour, which approximates the rate for IM1 and IM2. Similar values for IM2 and IM3 were 7.6 hours and a relatively higher value of 10.7 occurrences per hour. I tested for differences in the total number of supplanting occurrences observed for IM1 and IM2 and for IM1 and IM3 (14) and for IM2 and IM3 (81) with expected values generated from the number of hours feeding together (27.5 and 67.5, respectively). Assuming that the frequency of supplanting patterns is time dependent, differences are significant.[22]

In a comparison of head nibbling frequency among the three pairs, I found nibbling also occurred more frequently between IM2 and IM3 than it did between members of the other pairs, although differences are not statistically reliable. With the condor initiating the bout listed first and the frequency of occurrences per hour of non-feeding time—when both birds were present at the bait—noted in parentheses, the tally of head nibbling occurrences are as follows: IM1-IM2, 1 (0.5); IM1-IM3, 2 (0.8); IM2-IM1, 1 (0.5); IM2-IM3 1 (0.1); IM3-IM1 (0.4); and IM3-IM2, 11 (1.2). The behavior of these birds suggests that the tempo of social activity between condors may depend in part on the extent of social experience with each other.

Head nibbling. Many of the interactions between immature males standing around the Colombia bait area involved head nibbling. Of the 12 nibbling interactions noted between IM2 and IM3, five occurred in the context of a "greeting." Four times, I saw IM3 walk uphill from the bait and nibble at IM2's head just after IM2 had landed. The reverse occurred only once. However, IM3 landed at the bait only nine times when IM2 was already present, whereas the reverse occurred 35 times. The proportion of these reciprocal "greeting approaches" for the two birds (1:4) paralleled that of the available contexts (9:35). However, IM3 initiated all of the six observed head nibbling incidents for those periods when the pair stood and walked about in the general area around the bait. Most of the nibbling interactions lasted only a few seconds. A number of them ended when one condor began nibbling more harshly and the other pushed him away with a foot pressed on the breast or head of the nibbling bird.

Female Relations

I saw immature females infrequently so I have little quantitative data describing their relations with immature males or with each other. Most of the observations concerned interactions at the Colombia baits between IM3 and either IF1 or IF2.

Encounters between IF1 and IM3 usually were agonistic. Frequently, I saw IM3 peck IF1 on the head while she fed. Once she pecked him on the neck while he was feeding and then he pecked her before feeding again. On another occasion, she jumped on his back and slid off when he leaped forward.

The reactions of IF2 and IM3 were also rather aggressive even though IF2 was older than both IF1 and IM3. Once, when IF2 landed at the bait, IM3 immediately landed behind her and attacked her. They bit and jumped at each other with wings flapping for several seconds. When they stopped fighting, IF2 walked toward the bait. IM3 ran and pecked at her, and she flew. On one occasion, he chased her from the bait four times, running at her with open beak; yet later that

day, these two birds fed together. At one point during the feeding bout they stopped and nibbled at each other's heads for a minute before returning to feed. In a 10-minute nibbling interaction observed in the Cerro Illescas between a sub-adult male and a stage-2-immature female, the two birds lay on the ground facing each other with the full length of their necks extended across the ground as they nibbled at each other's head, neck, and back.

Immature males supplanted immature females more aggressively in Colombia than on Isla Zárate.[33] Most of the approaches in Colombia, however, were by only one immature male, IM3, and might not be representative of interclass supplanting relationships for that area.

Data on the intraclass relationships of immature females were limited to only a few observations. In Colombia, I never saw more than one immature female on the ground at the bait; they seemed to prefer visiting it when no other condors were present (Figure 24). At the Cerro Illescas in Peru, I once saw a sub-adult female and a stage-1-immature female fight suddenly after a short head nibbling bout. The sub-adult stood on the immature bird's back at one point and bit at her head before the younger female ran out from under her and away to end the struggle.

RELATIONS IN THE AIR AND ON THE PERCH

Adults and Adults

Associations in the Air

Associations in the air between adult males and adult females were pronounced in Colombia where birds were resident (Appendix B). Associations and other relationships between members of two specific pairs in Colombia are discussed in detail in Chapter 4. Flying adult males and adult females were also associated with each other on some parts of the Peruvian coast. Because this coastal population was probably of a transient and non-nesting status,

evidence for associations there suggests that pair bonds persisted during periods of large scale movement (> 80 m to any feasible nesting areas). Observations on pair 2 in Colombia also indicate that pair bonds extended beyond the period of nesting; these two adults mated frequently and traveled together but did not nest during a 4-month period of observation. Pennycuick (1972) described formation flying by griffon vultures where groups of up to 50 birds circle together, usually in the vicinity of breeding sites. I saw no evidence of such extensive breeding-site associations with the Andean condor.

Aerial Pursuits. Except for positive associations in flight, aerial pursuits represented the only other relationship recorded for flying condors. The majority of pursuits I observed consisted of short dives, but a few lasted for 20 minutes and crossed ground distances of up of 20 km. In one adult male-adult male chase, the crop area of the pursuing male seemed more yellow in color and more expanded than usual; the pursuit consisted of eight diving flexglide patterns by both birds and lasted 3 minutes. During one unique adult male intraclass chase, the lead bird landed on a cliff three different times, taking off each time when the other, in a steep S-shaped descent, dove toward him. The first time the pursued bird landed he appeared to pull several beakfuls of grass before he flew. The pursuit ceased after 15 minutes, and each male glided away in opposite directions.

Frequently, an adult swooped toward another adult standing in a feeding area; the latter usually took off and other pursued. Once I saw an adult male cross the Pasto canyon in a fast 1-km-flex-glide (a gliding pattern with partially flexed wings) directly toward the bait where an adult female was feeding. When he was within 100 m, she took off and dropped rapidly into the canyon. He followed. On Isla Zárate, an adult male dove in a flex-glide toward a feeding adult female. As she was taking off, he struck her in the back with his feet and bit at her. Koford (1953, p. 32) noted chases by adult California condors that sometimes extended from one perch

to another. He also noted several chasing flights between members of a nesting pair (p. 96); I never observed this with Andean condor pairs that were known to be nesting or mating.

In pursuits by class-identified Andean condors, adult male-adult female interactions were seen most often. Of 84 pursuits observed between two birds of a known sex and age class, 43 (51 percent) were of adult males pursuing adult females (Table 35). The high frequency of these intersex chases might reflect the clear dominance of adult males over adult females as characterized in their feeding relations. An intraclass hierarchy would limit the number of possible pursuits if birds that were subordinate according to supplanting activity never pursued dominant birds. Yet any male could pursue any female. Only nine adult female intraclass pursuits were recorded, compared to 21 for adult males, a difference possibly related to male-specific aggressiveness. In general, intraclass pursuits by adult females seemed to involve less turning, flapping, and actual contact than those between adult males.

Three-bird Pursuits. I recorded 13 different pursuits in which three adults were involved. On Isla Zárate, I saw an adult male land near two other adult males that were fighting. They all took off at once and, in flapping weaving flight, disappeared one after the other around the other side of the island. In each of the remaining 12 instances, an adult male and adult female pursued another adult.

Most of the chases were observed in the vicinity of an occupied nest in Colombia, where three adult pairs roosted in the same 1-km^2 area. Usually, pair 1 pursued another adult. I once saw AM1 chase another male in front of roost area 1 for 15 minutes. AF1 joined the chase as they repeatedly ascended up to the rim of the canyon and descended 400 to 500 m into it. A cow had fallen from the rim near roost area 1, and condors were feeding upon it. The pursued male might have left the area and evaded pair 1 earlier had there been no available food.

Relationships on the Perch

Associations of perched adult condors were notable, especially in the Paracas area. Although three adult pairs roosted in a 1-km^2 in the Colombia study area, each pair used a different cliff; in contrast, at Paracas, condors roosted in groups of up to 15 birds on the same cliff face (Plate 25). In both areas, condors sometimes perched so close to each other that they almost touched. Peruvian condors not only congregated at the night roost sites but also at day roosts. Over one 4-day period three to seven condors perched together each day on one Paracas cliff, below which lay a dead sea lion. Although they used a different part of the cliff each day they always perched within 10 m of each other. Once three adult females and an adult male all stood within 3 m of each other. California condors often roost in groups on cliffs or in stands of trees (Koford, 153, p. 36). Goodall *et al.* (1951) reported an observation of five Andean condors perched together in one tree in southern Chile. These social roosts may function as information centers for locating food, where condors successful on one day lead others the following day (Ward and Zahavi, 1973, see also the section in this work on dominance).

Interactions among perched adults were common, particularly between males and females. Nibbling occurred occasionally among perched adult pairs in the Colombia study area and in the Cerro Illescas. In the Colombia area courtship postures and copulations were also frequent. Once, in Colombia, I saw an adult male step onto and over the back of an adult female standing with him on the same ledge; she male no apparent response.

Condors perched together on the same ledge occasionally supplanted each other from particular sites. I once saw an adult male jump at another adult male and displace him from a cliffside perch. The second male walked about 5 m to another ledge. On another occasion, an adult walked up to and supplanted another adult from a rocky point. Then, in the same fashion, a third adult left when approached by the second. Both displaced birds flew. Once an adult female attacked another after the two had roosted together—along with an adult mal—within an

Plate 25. A group of thirteen condors on the roost in the Paracas study area.

area 6 m^2 on the same cliff. After the quarreling females flew, the male took off. In 3 minutes, he landed, and one of the females alighted 1 m from him. The second female ascended in circling flight and then flex-glided into the distance. These condors were probably the same three observed in aerial pursuits in that area the day before. Perhaps the females were competing for a mate. Adult California condors sometimes displace one another from perches and occasionally a fight breaks out (Koford, 1953, pp. 31-32).

At a Paracas roost I once witnessed an instance where visual signals would have been appropriate among the condors gathered there, but I failed to detect any signs that information was transferred. Three condors perched on the roost, and four flew nearby. All of the flying birds and two of the perched birds saw me immediately. An adult female, lying on a sandstone ledge, stood and took off within 1 minute of my arrival. A perched adult male with neck extended watched me closely. Another perched adult male apparently did not see me until I stepped nearer 5 minutes later. He did not seem to respond to any signals that might have come from the other six, even though he saw the female take off and watched the circling adults watch me. When he did see me, his posture changed as well. He stood more erect and extended his neck toward me.

Adults and Immature Condors

Associations in the air between adults and immature condors were rarely seen. In the Colombia area I saw a sub-adult female circling and flex-gliding with a particular adult male recognizable by a molt pattern in the tail. Then, 17 days later, I saw them foraging together once more. Except for these two instances, I did not recognize the two birds again, either alone or together. The female may have been sexually mature but had not yet undergone the final molt to adult plumage. On one other occasion in that area, I saw an adult male and a stage-1-immature

male circle together in the same general place for 15 minutes. Twice, they perched together on the same ledge; once, they stood only 60 cm apart for 5 minutes, yet no pursuits or instances of parental feeding occurred during the observation. Nevertheless, the young male may still have been dependent on parental care.

Most aerial pursuits were seen in Colombia in the near vicinity of an occupied nest and involved an immature bird and a member of the nesting pair (2).

A number of other adult-immature pursuits observed involved three birds. On the Paracas peninsula, I saw an adult and an immature bird in pursuit of another immature condor. After several minutes, the adult glided away, but the two immature birds continued the chase for an additional 2 minutes. In the remaining 2 minutes. In the remaining three-bird pursuits seen, two adults--a male and female in those instances where both were identified--chased one immature bird. During one 2-day observation period in Colombia I watched one pair of adults repeatedly chase an immature male condor that frequented their roost area after a cow had died nearby. On the first day, I saw the pair chase him off a cliffside perch five different times; aerial pursuits by both adults followed in three instances. However, on two different occasions during the day the immature birds landed within 5 m of one of the adults and remained perched there for periods of 5 and 37 minutes before one of the adults chased him again. On the second day, I saw another five pursuits involving the same birds.

Although adult and immature condors sometimes perched together, segregation seemed marked in other instances. I saw 11 adults in the Paracas area perched on one cliff, all within 15 m of each other, while 0.5 km away on another cliff four immature condors, two males and two female, perched together within 30 m of each other. I saw no pursuits. According to Koford (1953, p. 32), immature California condors tend to perch together. Segregation might proceed directly from dominance relations. On three separate occasions in one Peruvian area, I saw an

adult supplant an immature bird from a perch.

Immature Condors and Immature Condors

I obtained little data on interactions among immature condors in the air or on the perch. In Peru, I saw only one encounter, a pursuit. A stage-2-immature female flew about 30 m above a stage-1-immature female feeding on a Paracas beach; the latter flew, and the older bird chased after her for about 100 m. In Colombia, IM2 and IM3 often flew together. When IF2 and these two males were in the bait area, they frequently circled together. I saw IF2 and one of the young males perch together within 1 m of each other once. Circling patterns by the immature birds were often interrupted by brief pursuits. Once, IM3 was pursued by another immature male, presumably IM2, for several minutes in five long diving maneuvers. In general, these pursuits flight patterns seemed less stable than those of adults. Koford (1953, p. 32) reported that adult California condors on the perch tolerated each other and immature birds more than immature condors tolerated each other; perched immature birds frequently fought. Sometimes they fell, and one pursued the other in flight. I did not observe this relationship with Andean condors.

SOCIAL STRUCTURE

Dominance

<u>The Intraclass Hierarchy</u>

In general, across-class dominance was clearly expressed in the social organization of the condors I observed. Within-class dominance hierarchies were also found, and not only among resident members in the Colombia study area, but apparently among the transient birds visiting Isla Zárate as well. In Colombia, AM1 always supplanted other adult males, and IM1 always supplanted other immature males. I could not recognize individuals on Isla Zárate, so I searched

for indications of unidirectional supplanting patterns by comparing intraclass supplanting rates according to the number of within-class members present (Table 34).

Assuming that different birds of the same class supplant at similar rates, one would expect that in the absence of a hierarchy, the mean supplanting rate per bird would be constant and independent of the number of within-class members present. As described earlier (p. 128-129), the rate of supplanting activity by dominant condors appeared to be independent of the number of subordinate birds present. If, on the other hand, a hierarchy existed among within-class individuals, one would expect the mean supplanting rate per bird to diminish with a reduction in the number of within-class members present. The minimum rate per bird would exist when only two condors were present, a condition in which only one condor would be supplanting. Within-class rates recorded when two adult males were present were significantly less than those recorded when there were more than two adult males present.[34] A similar relationship may have applied with adult females ($P < 0.10$).[35] Both relationships provide evidence of a within-class hierarchy among condors on the island.

According to Koford (1953, p. 62) adult California condors chased other adults and immature birds, but the immature condors only chased other immature birds. He was unable to identify them individually so the structure of their intraclass relations remains unknown. On several occasions in Peru, I saw turkey vultures involved in "supplanting rings," where A supplanted B, B displaced C, and C supplanted A. Once, instances of supplanting (most involving a leap toward the bird supplanted) traveled around a ring of three birds 11 times in 2 minutes. Loftin and Tyson (1965) described a "dance" by turkey vultures where this stylized circular displacing of one bird by another apparently occurred on a sandbar where no food was present.

Functions of Dominance: An Examination of Related Factors. Dominance assures

particular individuals a priority of access to a certain resource. Any reduction in potential danger and energy loss for contestants of a dispute is advantageous to both members, so long as the hierarchy established corresponds to the ability of individuals involved. If the latter condition does not hold true, individuals subordinate in a hierarchy but not in ability would be less fit than those in a similar situation that contested the hierarchy. A bird that sacrificed priority of access to a weaker cohort would not be as fit as a strong bird in a representative hierarchy. In other words, a means for detecting "cheating" is likely to be an integral part of any linear dominance hierarchy consistent as the Andean condors'. In this framework, a hierarchy advantageous to all members will be tested continually with most of the tests involving individuals similar in ability and similar in their demands for limiting resources. Assuming these conditions were fundamental in condor relations, I searched for individual factors that seemed to shape the structure of dominance expressed in their social organization.

Locality. Most of the aerial attacks by adults on perching condors were directed at other adults in the feeding area and at immature birds on cliffside roost and perch area. Considering only two-bird pursuits when the pursued bird was chased from the ground, I found in the feeding area that only 5 of 47 instances were adult-immature bird pursuits, the remainder being adult-adult pursuits; on cliffside roost and perch areas, 7 of 10 such pursuits were between adults and immature birds. The proportion of pursuits involving immature birds was significantly higher in the latter group.[36] Several times I saw an adult dive toward an adult and two immature birds at the bait and then pursue the adult into the canyon and leave the immature birds behind. These data came from the Colombia study area, where immature birds might well have been progeny of the pursuers.

Condors are often involved in aggressive interactions at the feeding area. If this condition operated during the evolution of the species, there may have been selection for an

ability to distinguish related companions, or birds likely to be related, from others. A condor that tended to pursue unrelated or distantly related members of the population could pass this pattern of selectivity on via the benefit of deference provided progeny or other closely related companions. The reverse condition observed in the cliffside roost and perch areas may have been a result of territorial relationships that were more stable among adults than between adults and immature condors. Many of these pursuits could have stemmed from repeated attempts by the younger condors to return to areas they once frequented as volant juveniles dependent on parental care.

Social experience. Younger, less experienced condors are more hesitant than adults in supplanting encounters. One hesitation response, remaining motionless at the feeding point for 5 or more seconds (pattern 5, Table 30), was relatively insensitive to the simple peck/jump approach dichotomy (Table 33) and tended to be associated with immature birds. On Isla Zárate, this pattern was employed relatively more often by immature condors than by either adult males or females to both simple and peck/jump approaches by adult males (Table 31, see footnotes 5 and 6 for tests of differences). This immature-specific hesitancy may be related, in part, to an overall reduction in the level of activity by immature condors at the feeding area.

In three comparisons, however, variation in the prominence of this pattern indicates that condors respond more rapidly in instances where mutual social experience has been extended and/or dominant-subordinate positions are explicit: (1) In Colombia, immature males hesitated at a peck/jump approach of another immature male more often than they did to the same approach of an adult.[37] (2) IM3 hesitated at the peck/jump approach of IM2 less often than other immature condors in Colombia did in other intraclass peck/jump encounters. Differences were reliable.[38] In this case, the extended close association of these two partners likely forged a comparatively explicit dominance relation. (3) Immature condors on Isla Zárate hesitated more

often than immature birds of Colombia to both simple[39] and peck/jump approaches by adult males.[40] Immature members of the Zárate populations may have had a slower response because, being transient birds, they had less experience with particular individuals. These condors probably are not subjected to territorial behavior patterns by recognized individuals on the island, whereas condors in Colombia probably were. Accompanying this apparent difference in responsiveness is the general tendency by Colombian birds toward less aggressive supplanting patterns and the response patterns associated with them.

The effects of social experience and maturity may, in some cases, act differently. Supplanting rates by adult males seemed unrelated to the number of subordinate birds (adult feathers) present (p. 128-129), yet movement from feeding site to feeding site by IM2 appeared to accelerate after IM3 arrived at the carcass. In the latter case, the subordinate bird seemed to act as a focus of attention that superseded feeding efficiency, whereas in the former, the presence of additional subordinate birds did not appear to affect feeding rates. The examples suggest that hesitancy in a supplanting encounter is depends on social inexperience, whereas the tempo of social activity between two birds, like the rate of supplanting, depends on youthfulness and social experience (see also p. 147).

Alertness. The degree of alertness at the feeding area may have some relationship with social rank order in supplanting activity. As noted earlier (p. 147), the rank order of dominance for three immature males matched the rank order of wariness, with the dominant as most alert. Wariness-dominance relationships for adult and immature birds were parallel. In general, adults were dominant over immature birds and were more wary. They looked up and around more often per unit time while feeding, and they seemed more sensitive to disturbances by black vultures. Alertness probably facilitates quick escape from potential dangers that exist outside of the condor social order, dangers most likely presented by man. If dominant condors have a

priority of access to food, they can afford to be more alert than subordinate birds. Selective pressure for any adaptations that aid in avoiding danger would affect dominant birds more than others if the adaptation conflicted in any way with the bird's ability to secure food.

Priority of access to food. In the Colombia study area, I found that adult females tended to carry less food than the dominant adult male. With Peruvian data, I tested for and found a positive relationship between dominance and a priority of access to food. A tabulation of the condors near a carcass and those actually feeding on the carcass on the Isla Zárate beach demonstrated that comparatively more adult males, the dominant class, were likely to be feeding at a given time than either adult females or immature males. Every 10 minutes, I recorded the number of condors on the ground and the number actually feeding. Assembled according to sex and age class, these frequency data depart significantly from the frequencies of the null model (Table 36). A larger percentage of adult males fed than either adult females or immature birds; the proportion of non-feeding birds varied directly with the numbers of condors present. Adult females were more common than members of other classes on the Zárate beach; if the number of feeding sites available on the beach were less than the total number of condors, the feeding ratio for the more ubiquitous females might have been reduced without reference to dominance effects. For this reason, I used four separate matrices to compare ratios for similar individual frequencies of the different sex and age classes. The marked relationship described is not surprising, because dominance is defined here by the direction of supplanting activity at food.

Fighting. If condors feed in class-specific manners and visit feeding areas according to class-specific timetables, competition for food should be more acute among members of the same class. Also, if most tests of dominance involve individuals similar in ability and similar in demand for certain resources, instances of fighting should occur relatively more often between within-class members. Such a trend was found. Of 23 recorded fights, 15 involved intraclass

Table 36. Age-sex class differences in the percent of feeding condors present on the beach (standing within 50 m of a carcass). Each occurrence represents a sampling taken every 10 min whenever two or more condors were on the Isla Zárate beach during 12 days of observation. Rarely were more than two immature condors present so they could not be included in the last two tests.

	Percent sampling occurrences						
	Percent present that fed						
No. birds present	0-20	21-40	41-60	61-80	81-100	No. of samples	Tests
1 adult male	24				76	34	
1 adult female	64				36	22	x^2 =10.24,
1 immature bird	50				50	90	$p < 0.01$
2 adult males	3		53		43	30	
2 adult females	17		50		33	18	$x^2 = 14.54$,
2 immature birds	32		18		50	34	$p < 0.01$
3 adult males	0	11		70	19	27	$x^2 = 10.45$,
3 adult females	21	24		36	18	33	$p < 0.02$
> 3 adult males	6	17	31	33	14	36	$x^2 = 22.67$,
> 3 adult females	12	40	27	19	2	52	$p < 0.001$

pairs (Table 26). Fights between adult females and immature males constituted five of the interactions. Here no clear case of class dominance exists. Only three of the 23 fights were recorded for contestants belonging to classes related in a clearly dominant-subordinate fashion. One sex and age class was considered clearly dominant over another when supplanting activity between birds of the two classes was always unidirectional.

Basic Elements of the Dominance Structure

Age-Sex class determinants. General levels of aggressiveness in interactions at the feeding area vary according to the age and sex of the birds involved. One can ask why it would be useful in an encounter for individuals of one class to behave in one way, whereas those of a second class behave in another. What use is it, for example, for a female to be relatively less aggressive than a male at the feeding area? To this general question of class differences, several hypotheses are presented: (1) Aggressiveness specific to one sex functions as a way to obtain mates or nesting areas and appears at feeding areas primarily as a consequence of this reproduction-based competition. (2) The hierarchy structure is characterized by dependent-rank relations. In this situation, a female of an adult pair might enjoy the dominant position of her mate when she is in his presence.

Intraclass supplanting incidents were characteristically aggressive for adult and immature males, whereas those of adult females were not; this difference suggests that conditions of the first hypothesis exist. Also, the evidence for territorial behavior indicates that aggressiveness may operate in the competition for nest area or mates. A few other observations also support the second hypothesis. On four separate occasions, I saw an adult female approach one adult male when another adult male approached her. In a number of three-birds pursuits, an adult female accompanied an adult male in pursuit of another adult male.

Limitations of analysis. Multiple comparisons of class-specific differences in

supplanting encounters are required to isolate the determinants of class structure in dominance. I was unable to secure such information, however, because interpretations of the data from interclass comparisons were ambiguous; characteristic differences in supplanting or response patterns could not be attributed to a single class. During the supplanting approach of one condor toward another the actions of each bird no doubt modify those of the other in a rapid and continuous manner perhaps to such an extent that the form of the supplanting approach itself is as much a response as the action of the supplanted bird.

To illustrate: I compared adult female supplanting patterns directed toward adult females with those directed toward immature males and found that approach patterns toward the males were more aggressive (p. 143). However, the differences in aggressiveness displayed by adult females may have depended on the response of the male. Immature males may be slower than adult females to respond to a supplanting approach (p. 159). If the appearance of aggressive components in the adult female's supplanting approach depended to some extent on the proximity of the other bird at some critical stage of the interaction, one might expect to find specific differences in the supplanting approach according to the class of the bird supplanted. In this hypothetical instance, the differences are due to characteristics intrinsic to the bird supplanted and not to the one supplanting. On Isla Zárate, adult male supplanting patterns directed toward immature males seemed to be more aggressive than those directed toward adults in general (p. 153); perhaps both adult males and adult females respond similarly to some specific motor component or component duration in the withdrawal pattern of the immature male.

The "Centripetal Attention" hypothesis. Chance (1967) characterized the fundamental feature underlying rank order relationships of primates as the "centripetal attention" of subordinate animals directed toward dominant ones. In the spatial organization of primates,

dominant individuals are usually central, while subordinates occupy peripheral positions. Positing this basic principle of attention, he argued, not only clarifies similarities in social organizations of different species but also does away with terms like "leadership," a condition, he claimed, that is more accurately assessed in terms of attention structure.

Two conditions in the social organization of the condor suggest that Chance's paradigm does not apply for this species: (1) On occasion, condors seemed to move from feeding point to feeding point on a carcass less frequently when alone than when a subordinate condor was present. Although I recorded no quantitative data to confirm this impression, I noticed a number of times that IM2 fed for extended periods at a single point until IM3 landed. Then IM2 supplanted IM3 repeatedly; the two of them moved from point to point, sometimes circling the bait two or three times. In this case, it appeared that the subordinate animal was the major focus of attention. (2) An examination of data on lead-follow relationships for two adult male-adult female pairs (p. 133) indicates that social activity is not always coordinated by efforts of the subordinate members as implied by Chance's paradigm. Landing or take off by either member of a pair seemed to induce the other to do the same.

Dominance and Sexual Dimorphism. The extent of sexual dimorphism seen in the Andean condor has no parallel among any of other vultures, New or Old World. Although male Andean condors are larger than females, the most obvious differences are on the head (see Plates 5 and 6). The larger size in males might be a consequence of male-specific competition for a mate or territory. This explanation, however, does not account for dimorphism of the heads. The individual differences in male heads, particularly crests, are marked: in Colombia, this attribute allowed us to identify individual males with ease. The crests flopped or tilted to one side or the other in a consistent manner, and the pattern of wart-like projections varied from bird to bird. Females bore no such individual characters that we could identify, and we were unable

to recognize any adult females individually except by molting patterns of feathers.

Irregularities in head shape may be useful to condors in the same way that it was for us, that is, for the identification of individual males. Individual recognition may be more important among males than females, because males are the dominant class. An adult females, permitted to feed with her mate, would share his dominance status; in such instances, discrimination of other female would be necessary. Establishing and maintaining a position in the well defined hierarchy may require less energy if condors, particularly subordinate males, are able to identify another male easily. As noted earlier, an instance of supplanting behavior observed for the monomorphic turkey vultures indicated the absence of a linear hierarchy there.

If stable residential populations were common in the evolution of the Andean condor, then this male-specific recognition would be of adaptive value. Regular fluctuations of food in particular areas, like, for example, concentration of breeding sea lions along the Peruvian coast, might foster avian population enclaves of avian scavengers that migrated as units on a regular basis. Dimorphism in the California condor and other Cathartidae might not have held the same advantage if past populations were more dispersed and ephemeral in individual composition. In areas where food appears irregularly and over scattered areas, individual recognition in avian scavenger populations may have played a relatively smaller role. Among other monomorphic Cathartidae a comparatively less rigid dominance structure between sexes is likely. If the success of any mated pair of these species depends at all on dominance relations, their relative position in the hierarchy probably depends on the status of both mates rather than only one, as with *Vultur*.

Andean condors are easily discriminated, not only on the basis of sex but on age as well. This condition, along with the clear dominant-subordinate positions of most sex and age classes, can encourage faster, more consistent recognition than is usually found in societies where

dimorphism is absent and the bird has a much greater number of birds, similar in appearance, to discriminate among. In east Africa, Houston (1976) reported a ratio of feeding attacks by first-year white-backed vultures on birds three years or older as 25:41 over the reverse condition, whereas the ratio of young to old birds present was only 32:68. That young birds ever attacked adults at all is in stark contrast to our observations of the condor, in which no instances, except those involving young males and adult females, were ever seen. In the Andean condor, the distinctions of both sex and age seem to be an adaptation for establishing or enhancing the orderly and accurate individual hierarchy that we observed.

Territoriality

In Colombia, the use of some areas by individual condor pairs seemed regular and exclusive. The three adult pairs that roosted in a 1-km^2 area rarely circled in front of each others' roost cliffs. Each pair appeared to have its own flight route in that locality. In the morning, each pair often ascended along the canyon wall in one of three different sites. Usually, they returned to the roost cliffs from three different directions, one specific to each pair. During the day, pairs 1 and 2 each restricted their perching to 15 to 20 different ledges, all within 400 m of their own roost site. Although the two areas were adjacent on one canyon wall and the nearest perch sites of the two pairs were within 100 m of each other, I never saw, in 60 full days of observation, a member of one pair land on a perch used by another. The two pairs each used two different pools for drinking and bathing. Situated on ledges near each pair's roost they were only 0.5 km apart. I never saw one pair use the pool in the other's area.

On the coast near Paracas, condors of the same sex and age class regularly roosted and fed together, whereas adult males and adult females in Colombia seemed to avoid others of their own age-sex class, not only at the roost but at the bait as well. "Parceling" resources, in effect,

this phenomenon may be characteristic of resident populations. The seemingly exclusive use of the perches and the bathing pool in the roost area of pair 2 suggests that aggressiveness in the response of one or both members of pair 2 to an approach by members of pair 1 would have varied according to the locality of the encounter. Although AM1 supplanted AM2 at the bait and may have pursued him in the air, AM1 was never observed to land near the nest area of pair 2. The possibility of an aggressive contested encounter with AM2 probably influenced the actions of AM1 in avoiding the use of perches in the nest area.

A few interactions between these pairs are noteworthy. Pair 1 once flew to within 100 m of where pair 2 was perched on their own roost ledge. Af2 took off, and AM2 stood from a lying posture. He lay down again in several second as AM1 and AF1 returned to their roost area. On another occasion, pair 1 flew near pair 2 when they were perched on their roost ledge, and both birds took off. They landed together 150 m away on another ledge, and AM2 immediately assumed a courtship posture for 6 seconds while the other pair returned to their area. Courtship postures by this male were relatively uncommon, and in this case may have been a response to the approach of the other pair. Twice, AM2 chased one male, a member of a third pair that roosted nearby, from the vicinity of his nest to a ridge that separated the two areas frequented by each pair. The marked black and white plumage of the adult condor may be an adaptation for establishing and defending a territory; immature birds are cryptically colored.

With turkey vultures, Davis (1979) noted a parallel condition where birds may have been defending an immediate nest area at locales near a social roost. Ten times during the pre-roosting period, the time of day when adults were most conspicuous in the nest area, she saw breeding birds dive at others in six instances and lock feet momentarily with another in one pursuit. Yet sex of the eight nests she found were within 1-2 km of a social roost. In another study area, she reported that aggressive encounters at a social roost declined by a factor of five

from the period of June to July (Davis, 1974); the timing of this heightened aggressiveness with the onset of nesting suggests that reproductive competition was an ultimate factor. Ward and Zahavi (1973) argued that social roosts often function as information centers for finding food. They contended that information about food is advertised when the distribution of food is patchy, when there is too much for an individual to consume, and when the food will disappear quickly anyway. Such conditions may well prevail in vulture societies and explain the tendency toward social roosting in *Vultur* and *Cathartes,* even though territoriality may still operate.

The narrow spatial setting for these observations suggest that the behavior is locality-related, the central element in the concept of territoriality. Aerial scrutiny of humans by adult condors tended to be a male-specific response, a consequence, perhaps, of territorial behavior by males. All of six instances observed where a condor dove toward and pursued a black-chested buzzard-eagle occurred less than 200 m from the nest of the condor pursuing. Steward (1974) watched an incubating black vulture leave its nest in an abandoned building, chase an intruding turkey vulture from the building, and then return at once to its nest.

Some expression of territoriality may occur with captive condors. Gailey and Bolwig (1973) noted that the male condor of a captive nesting pair attacked the keeper only during the middle of the breeding season and then only when the keeper approached the nesting site. In Old World vultures, Pennycuick (1972) reported aerial fighting by lappet-faced vultures as some evidence for territoriality over a rather restricted home range. He saw no long cross-country flights by members of this species, as he did with griffon vultures. Griffon vultures follow herds of migrating ungulates for food and apparently do not hold any feeding home range or territory (Houston, 1974a).

CONCLUSIONS

This chapter described patterns of interaction observed at feeding sites, as well as at perches and in the air, and considered characteristic variations for different individuals, age-sex classes, and populations. Some fundamentals of social organization were examined as possible determinants and functions of the dominance hierarchy.

Dominant birds appeared to be characteristically wary. With a priority of access to food, dominant condors could afford to be more wary than subordinate birds if the wariness conflicted in any way with the bird's ability to secure food. Priority of access to food by dominant birds was obvious on Isla Zárate; within any one group, adult males were more likely to be feeding at a given time than adult females or immature birds.

Aerial pursuits and a partitioning of areas provided some evidence for territoriality. Although one nesting male was subordinate to a particular non-nesting male at the bait, an exclusive use of adjacent perch, roost, bathing, and drinking areas on a single canyon wall suggests that any attempt by the non-nesting male to land near the nest would have been contested. The non-nesting male frequented the same general area. In contrast, groups of up to 15 condors of all classes perched together during the day and roosted together at night in the Paracas area, where the birds were transients and probably not nesting.

Most aerial attacks by adults on perching condors were selectively directed at other adults in feeding areas and at immature condors on cliffside roost areas. Some of the pursuits in the roost areas probably resulted from attempts by young condors to return to areas they had frequented as juveniles when dependent on parental care. Adults may have pursued other adults selectively and feeding areas, because they were less likely to be progeny or kin and, as such, represented a greater competitive threat.

Supplanting activity, in which one bird displaces another at a carcass, was the most conspicuous interaction observed at the feeding site. Social nibbling, a pattern possible derived

from the peck-and-parry supplanting encounter, may help suppress overt aggression when condors meet, whereas fights might serve as tests for clarifying dominance positions; only a small proportion of the fights observed (13 percent) involved contestants of classes related in a clearly dominant-subordinate fashion.

Dominance was defined by unidirectional supplanting activity. In most interclass comparisons, the dominance relationships were simple and direct: Adults were dominant over immature condors, and males dominated females. For immature males and adult female, dominance relationships reversed as the young males matured. Males were characteristically more aggressive with each other than were females. Adult males appeared to avoid other adult males, and adult females avoided adult females, whereas positive association were found between adult males and adult females and among immature condors, male-male relationships in particular.

Ten separate supplanting approach and response patterns were recognized; most of them were grouped according to two categories, so that the relationships between certain condors or classes of condors could be characterized. Although both categories of supplanting patterns, like the ten specific classes, are defined in descriptive terms, they can be viewed as separate levels of aggressiveness. Even though response patterns are less easily categorized according to levels of intensity, the frequency of most response patterns depended markedly on the aggressiveness of the approach. By this association, I ascribed a level of intensity to the responses. In general, condors withdrew from the carcass and ceased feeding, at least briefly, when supplanted aggressively, whereas nonaggressive approach patterns usually ended with a supplanted condor moving to another feeding site on the carcass.

Hesitancy in the response of supplanted condors tended to occur among birds with less social experience; a hesitancy in withdrawal from a feeding site after being supplanted occurred

more often with immature birds in specific and with birds of Isla Zárate in general. Supplanting interactions of the resident population in Colombia were more rapidly executed and smoother than those of the birds in the transient populations visiting the Peruvian island. Parallel to this difference was the general tendency by Colombian birds toward less aggressive supplanting approaches and the response patterns associated with them.

In the Colombian population of individually recognized condors, the dominance hierarchy, as determined by supplanting activity, was unidirectional and linear for within-class members as well as across-class birds. A test of differences in intraclass supplanting rates for different group sizes provided evidence for the presence of a within-class hierarchy on Isla Zárate as well. In dominance relations at the food and in the coordination of activity between members of an adult pair, no one condor or class of condors seemed to sever as a focus of attention for others.

The social structure of *Vultur* seems extraordinarily stable and rigid compared to other vultures, both Old and New World species. At our baits, feeding relations of *Coragyps* usually seemed no more than a sustained melee where fighting occurred almost continually and struggling was a more common activity than actual feeding. With turkey vultures, peculiar supplanting rings indicated the absence of a stable linear hierarchy. In feeding groups of Old World vultures (mostly of the genus *Gyps*), which I have seen on film taken by members of the Vulture Study Group in South Africa and Rhodesia, and by Michel Terrassee in Spain, the relationships seemed much like those we observed with *Coragyps*, where the orderly succession of feeding birds was absent. For white-backed vultures, Houston (1976) reported instances of young birds attacking adults; this was never seen with *Vultur*. Valverde (1959) noted that dominance in *Gyps fulvus* apparently depended on hunger; he described the continual struggles and shifting relationships among those that had fed and those that had not. Although hunger of

some critical level might affect a *Vultur* hierarchy, we found no evidence of any breakdown in the hierarchy during our study. In the recording of over 1500 supplanting encounters, we never saw an instance of a supplanting reversal (where one bird first supplants and then is supplanted by another) among (1) identified individuals or (2) among condors belonging to classes with clear dominance relations. Parallel to this marked difference in social orders between the Andean condor and other vultures is the unusual feature of distinct sexual dimorphism.

Clear interclass dominance relations in *Vultur* are likely related to the evolution of sexual dimorphism in the head shape. Variability in head shape probably allows faster and more accurate individual recognition among the males, the dominant class. Dimorphism in other vultures might not have occurred if individual composition of those populations tended to be more fluid and ephemeral, to the point that the organization of a clear hierarchy among different sex and age classes and individuals could not be sustained.

CHAPTER 6 RELATIONSHIPS WITH OTHER ANIMALS

INTRODUCTION

In Colombia, black vultures accompanied condors at the bait, whereas turkey vultures shared food with the condor in the Paracas area. In the Cerro Illescas, all three New World vultures fed together (Plate 26). This variety of feeding associations permitted us to examine in detail the relations among condors and other avian scavengers at food. The major objectives of this work were to determine to what extent interspecific behavior was locality-related and, if so, what factors contributed; to compare interspecific behavior and ecological differences for Old and New World vultures; to determine how dominance and fighting operated in the social organization of several of the monomorphic Cathartidae; and to describe relationships between condors and other animals.

Black vultures seemed to have little fear of the condors and fed in close proximity with them. Occasionally pecking and pulling at feathers of the feeding condors, the smaller vulture even appeared to harass the larger bird,. Compared to immature condors, adults were less tolerant of black vultures; nevertheless, they inflicted little injury on the smaller bird even when there were many opportunities to do so.

Turkey vultures were more retiring in nature and did not approach feeding condors. They fed at the same carcass with a condor only when feeding sites were some distance apart, well out of pecking range. Fights among black vultures and turkey vultures were much more common than those among condors; yet across-species fights among the smaller vultures were rare. In general, turkey vultures seemed dominant over black vultures when they fed together. To verify and describe these impressions, we gathered quantitative data, and I analyzed them for significant trends. The first part of this chapter is an account of the work dealing with

Plate 26. A subadult male condor makes a pecking motion toward black vultures at a bait in the Cerro Ilescas. Note the turkey vultures in the foreground.

relationships of the three New World vultures. A second part reviews studies of six species of Old World vultures, chiefly in East Africa, and compares relations among them and their environment with those of the vultures studied here. In the last part of this chapter, relationships between condors and other birds and mammals are considered, mostly on a descriptive basis.

RELATIONSHIPS WITH OTHER CATHARTIDS

Black Vultures

Positive Associations

Black vultures seemed drawn to the area around perched condors, not only in the immediate area of the carcass, but also on the hillside above the baits where condors landed and took off. Once, five black vultures flew from the carcass to land within 3 m of IM2 and IM3 after the condors alighted on the hillside above the bait. On another similar occasion, eight black vultures walked up to the pair of young males and followed them to the bait. Three times, IM2 pursued one of the vultures for a distance of 6 to 10 m; when this condor picked up a small chunk of skin torn from the bait, four black vultures approached to within 1 m, and, when he looked off to one side, one of the vultures moved to within 30 cm of the condor's feet. IM2 lowered his head, and the vulture scrambled away. Once, when IM1 nibbled at a ball of hair from the bait, a black vulture crept up and pecked at it twice before running off. The ball had been left untouched by black vultures until the condor nibbled at it. Several members of one group of six black vultures approached and nibbled at the tail and primary feathers of IM2 just after the condor landed above the bait. When the captive immature male condor was released for an hour's exercise in an area just south of Tumbes, Peru, a turkey vulture circled above and two black vultures landed beside him. Perhaps these smaller vultures are attracted to condors

because their presence on the ground is usually associated with available food. In East Africa, Kruuk (1967) reported that alighting vultures often enticed other vultures, particular griffon vultures, to land, even when food was not anywhere near. He cited these observations as evidence that vultures follow other vultures to find food.

Supplanting Relationships at Food. Feeding condors frequently made pecking motions toward black vultures (Plate 26). Recorded frequencies varied from an average rate of 3.5 pecking motions per minute by each adult female in Colombia to 0.3 per minute by each adult male in the Cerro Illescas (Table 37). These patterns ranged from rapid biting motions to movements with head and neck extended forward and the beak held open from 1 to 4 cm at the distal end for 1-to 2-second periods. Usually the long axis of the body was horizontal, with the extended neck also parallel to the ground. Sometimes the condor's body rotated to one side as the neck extended forward, but frequently the neck only turned to the side when condors bit at vultures standing alongside. I saw IM3 extend his inverted neck and head posteriorly between his legs to bite at a black vulture that stood beneath his tail. Sometimes condors ran with lowered head and neck toward black vultures; usually, one or both wings of the running condor were partly or fully extended. Occasionally, an adult male attacked black vultures by biting and leaping with both wings and legs extended toward the black vultures. Black vultures evaded the pecking motions by backing up quickly, turning and running, or hopping to one side. Some pursuits began when a sitting condor jumped up and ran toward the smaller vulture. Usually, the condor returned and resumed feeding in the sitting position.

In Colombia, adults, particularly females, were more aggressive toward black vultures than were immature condors (Table 37). On the average recorded frequencies of pecking at black vultures were higher for each adult female in Colombia (3.5 per minute) than for adult males (2.0 per minute), and adult male rates surpassed those of immature birds (0.8-0.9 per

Table 37. Frequency of condor pecking motions directed at black or turkey vultures while feeding at the baits.

Condor sex and age class	Frequency of observations for the following no. pecking motions per 5-min sampling period									Total no. sampling periods	Mean no. pecking motions per min
	0-1	2-3	4-5	6-7	8-9	10-11	12-13	14-15	≥16		
Colombia:											
Adult male	0	1	0	1	2	2	2	2	0	10	2.0
Adult female	0	0	0	0	0	0	2	1	4	7	3.5
Immature male	10	6	2	2	3	1	0	2	0	26	0.8
Immature female	5	2	3	0	2	0	0	1	0	14	0.9
Cerro Illescas:											
Adult male	2	1	1	0	0	0	0	0	0	4	0.3
Adult female	2	1	1	0	0	0	0	0	0	4	0.4
Immature female	3	1	0	2	0	0	0	0	0	6	0.6

minute).[2] Rate differences for immature males and females were not significant. Perhaps part of the variation between adult and immature birds can be explained by the differences in alertness. Because adults looked up more often, they had more opportunities to drive off potential harassment. Although the difference in rates of head raising between adult and immature condors was less than twofold (Table 45, pecking rates at black vultures by adults were more than twice that of immature birds--3.5, 2.0: 0.8, 0.9 (Table 37); thus, part of the variation in levels of aggressiveness between condor age classes cannot be explained by the variation in alertness. Adults also seemed to be more aggressive in driving off the smaller vultures. Neither adult males nor adult female condors pecked as frequently at either black or turkey vultures in the Cerro Illescas as they did at black vultures in Colombia.[3] Variation in behavior by the smaller vultures may have accounted for the difference. In the Cerro Illescas, both species, particularly turkey vultures, stood farther away from feeding condors than did black vultures in Colombia.

Biting. I saw condors of all sex and age classes bite black vultures, sometimes with enough force to pull out feathers. Vultures were usually bitten on the wing, but sometimes they were struck on the back, neck, or head. Bitten birds were often thrown to the side. Condors released the vultures quickly, even though they could have inflicted more damage. I never saw blood drawn. Many of the pecking patterns appeared to be gentle nibbles.

A series of patterns by IF1 in one observation period illustrates the variety and apparent impunity of most contacts. In the most common pattern, she lightly held the wing of the vulture as he moved away and then released it. In the second pattern, also used frequently, she extended a nibbling beak toward the black vulture and pushed him gently with the dorsal surface of the upper mandible until the smaller bird moved from the feeding site. Only once in this one observation period did she bite a vulture wing with enough force to shake the bird.

Biting attacks by immature condors were characteristically less forceful than those of adults. On many occasions, I saw black vultures feeding so close to immature condors that beaks almost touched. Once, IM2 fed with his head resting on the back of a black vulture that fed in the same hole. After several seconds, he bit the black vulture on the back and pulled him away; the vulture ran off to the side. In one feeding site, the beaks of two immature male condors and four black vultures fed in an area only 15 cm in diameter. The age-difference in toleration seemed apparent to the smaller vultures for they avoided adults more carefully than they did immature birds.

Harassing by Black Vultures. In one peculiar pattern commonly seen in Colombia, adult or immature black vultures picked at or pulled feathers of condors. Crissum feathers were pulled at most often, followed by secondary wing feathers and wing coverts. Less frequently, the smaller vultures nibbled at feet, tarsi, crus, tail, neck, or head. Most of the motor patterns observed seemed to be gentle manipulations, although occasionally they appeared to dig into the feathers, bite, and twist sharply. These patterns occurred frequently in Colombia, at an average recorded rate of 0.5 occurrences per condor minute when condors were feeding (Table 38).

I could find no marked preference by the black vultures for any particular sex or age class of condors. Sometimes the smaller vultures approached and nibbled at condors that stood quietly away from the bait, although rates seemed to be highest when black vultures clustered around condors that had just opened a new feeding hole in the carcass. In one 4-minute period, I saw four different black vultures pull at feathers and nibble at the legs of IM3 in nine separate instances. I saw a black vulture in the Cerro Illescas bite a feeding turkey vulture on the tarsus. The turkey vulture turned without pecking. The black vulture left, and the other resumed feeding.

Responses by the condors varied. Some birds continued to feed without apparent

Table 38. Frequency of feather-pulling and biting of feeding condors by black vultures at the Colombia baits. Usually about 20 black vultures were present.

Condor sex and age class	Frequency of observations for the following no. biting occurrences per 2-min sampling period						Total no. sampling periods	Mean no. biting occurrences per min
	0	1	2	3	4	5		
Adult male	8	1	2	1	2	0	14	0.6
Adult female	4	2	0	1	0	1	8	0.6
Immature male	16	13	13	0	4	2	48	0.7
Immature female	6	3	0	0	0	0	9	0.2

response. Others, feeding in sitting positions, stood, turned, ran, and sometimes bit at black vultures standing nearby. In general, adults, particularly males, appeared to be more aggressive in their responses. When a black vulture nibbled at the crissum and tail and wing feathers of IM3 as he sunned, the young condor's sole apparent response was to turn his head back and look toward the nibbler. Several times, I saw no apparent response by feeding adult females or immature birds when vultures bit at their wings. One adult male ran 2 to 5 m, in five consecutive rushes to pursue black vultures that pulled at his wing secondary feathers. In two of these instances, one immature black vulture was the offender. In another situation, when a black vulture pulled at the tail of a feeding adult male, the vulture, apparently anticipating the pursuit that followed, ran backwards as soon as the condor lifted his head,.

Infrequently, pecking motions directed by black vultures toward condors were notably aggressive. A black vulture bit IM1 on the head, and the young condor backed away. The small vulture fed in the site used by the condor for 20 to 30 seconds before the condor returned. IM1 bit at the black vulture, and then resumed feeding as the black vulture moved away. After IM3 had pecked at IF1 several times, a black vulture sitting on the neck of the bait horse also pecked her head twice. She bit at the vulture in return, and he left. One black vulture approached an adult male condor standing on the hill above the bait and bit one of the condor's primary feathers. The condor jumped away from the vulture.

On nine separate occasions, I saw black vultures jump up onto the backs of feeding immature condors and stand there for 1 to 8 seconds. Usually, the vultures slid off when the condors stood erect or ran, although once IM3 walked about for 4 or 5 seconds before the small vulture slid off. Only one of these observations involved a female condor; a vulture that jumped onto the back of IF2 pulled at her back feathers until she stood, and the vulture fell off. Six of these instances occurred on the same day and appeared to involve more than one black vulture;

social factors may have contributed. Population differences in feeding proximity between condors and black vultures in Colombia and in the Cerro Illescas also suggest a role of social stimulation in the group behavior of black vultures. Harassment is not peculiar only to *Vultur* and *Coragyps*, nor to New World vultures in general. In Europe, the common raven harasses the European griffon vulture by pulling feathers and leaping upon its back (M. Terrasse, pers. comm.); in Africa, pied crows treat cape vultures similarly (R. Friedman, pers. comm.).

With condors and black vultures, the function of harassing seems to work as an inducement for the wary condors to leave the bait area earlier than they would otherwise. Condors departing earlier leave flesh in newly torn holes accessible to the black vultures. Condors pursuing black vultures frequently ran after those standing alongside. Several times, I saw those black vultures that had nibbled at the crissum of a feeding condor step into the vacated feeding site after the condor turned and pursued black vultures standing alongside. If this pattern of response were common, it would seem to be advantageous to pick at the posterior part of the condor, a trend that was observed. The function of forcing earlier departures by condors does not seem to explain the instances of feather-picking away from the carcass unless food competition between the two species is so great that anything that induces a condor to leave is of benefit to the individual black vulture. Once, when a black vulture bit the wing of IF1 just after she landed, she shook her wing, knocking the vulture loose, and then she flew.

Food Struggles. Whenever condors wrenched free any large pieces of flesh that they were unable to swallow immediately, they ran backwards with bands of black vultures, usually 5 to 20 in number, in pursuit. Unable to fend off black vultures while swallowing, condors attempted escape, usually with success. Once, AM1 pulled out several meters of intestines, and black vultures mobbed around the newly exposed food. The condor dropped the intestines, chased the vultures away with open beak and wings, and leaving the intestines to the vultures,

returned to feed on the bait. In another instance, when two black vultures pulled at opposite ends of a strip of skin, an immature male condor grabbed the skin in the middle. One black vulture dropped it, and the condor ripped it free from the other. Then the condor walked to the bait, dropped the strip and left it.

Sound and Movement Disturbances. Condors often appeared frightened by the sounds made by black vultures. On a number of occasions, I saw condors run from the bait when the sounds of striking wings erupted from a struggle between two black vultures. Once, IF2 ran toward the canyon rim with wings partly open when two black vultures fought nearby; she returned, but then ran back again. In both cases, loud sounds from striking wings preceded her dash toward the rim. On her second return, she jumped at the fighting vultures and struck them with her feet. When black-chested buzzard-eagles glided overhead, black vultures rushed to huddle over the carcass; all condors present usually flew. I saw condors stand quietly beneath gliding buzzard-eagles on a few occasions when black vultures were not present; the bait departures described above apparently were stimulated by the sounds and movements of black vultures rushing together. Condors may have been alert to any disturbances possibly caused by man, their only major threat.

Study Area Comparisons. Black vultures did not feed as near condors in the Cerro Illescas as they did in Colombia. The difference in the rate of condor pecking motions directed at black vultures between the Colombia and Cerro Illescas was probably related to this difference in feeding proximity of the two species. We never saw any instances of feather-biting of condors by black vultures at the Cerro Illescas baits, although I once saw three black vulture nibbling at the feathers of a lone immature condor standing quietly out on a flat near the sea. The feather-biting pattern might only occur in those areas where wary condors were more likely to depart when harassed. Feeding condors appeared to be less wary in the Cerro Illescas than in

Colombia.

In Colombia, the number of black vultures at the bait averaged around 30 to 40 but sometimes went as high as 200. In the Cerro Illescas, about half as many black vultures came to the baits. Turkey vultures in the Cerro Illescas were slightly fewer in number than the black vultures,whereas in Colombia, they rarely visited the bait; I saw no more than two on the ground at once.

Turkey Vultures

When condors arrived,turkey vultures either retired from the carcass or moved to an opposite end. When the condors departed, the smaller vultures often returned immediately and fed in the openings torn by the condors. In the Cerro Illescas, where the three species of vultures fed together, black and turkey vultures fed together until condors arrived. Then, the turkey vultures moved off the carcass, often within 5 m, and watched while black vultures and condors fed together. I rarely saw a condor peck or jump at a turkey vulture, because the smaller vultures usually had moved off before condors were ever in pecking range. Koford (1953, p. 63-64) reported a similar relationship at food between turkey vultures and California condors; the smaller vultures moved away from the carcasses when condors arrived and returned later when the condors departed.

Like black vultures, turkey vultures may be attributed by condors on the ground, possibly as an indication of food nearby. On two occasions in the Cerro Illescas, I saw condors perched on the ground surrounded by turkey vultures, two birds in one instance and a group of 10 in the other. Once, on Isla Zárate, three adult and three immature condors roosted together with two turkey vultures on a cliff in an area about 7 m square. In Colombia, I saw AM2 pursue a turkey vulture in flight near the condor's nest area, where he dove at the smaller vulture twice without

striking it.

Turkey Vulture-Black Vulture Relationships

As a species, neither the turkey vulture nor the black vulture was completely dominant over the other at food. Individuals of each species supplanted members of the other. In a frequency tally of peck/jump approaches, however, I found that turkey vultures supplanted black vultures and other turkey vultures with about the same regularity, whereas black vultures supplanted turkey vultures less often than expected. I observed 18 instances of black vultures supplanting turkey vultures, compared to an expected value of 108 determined by tabulating the time species were together and recording the frequency of supplanting events (Appendix C). Part of the difference noted here might be explained by the effect condors had on the two species. Unlike turkey vultures, black vultures, probably dominant individuals, fed when condors were present. When condors left and turkey vultures began to feed, black vultures with unfilled crops were probably individuals subordinate in a dominance hierarchy, whereas the first turkey vultures to feed then were likely to have been dominant individuals. We recorded most of these data when condors were not or had not been present that day, so this possible bias cannot explain all the differences noted. In interspecific supplanting relations, black vultures displaced were often immature birds, whereas black vultures supplanting turkey vultures appeared to be adults. I did not differentiate age classes among the turkey vultures.

The observed frequency of contested fights between the two smaller species of vulture also diverged significantly from the expected. Interspecific fights were not observed, but intraspecific fights occurred frequently, particularly between turkey vultures. An occurrence of contested fighting was recorded whenever two individuals jumped and pecked at each other, making contact. None of 34 fights observed involved members of both species, yet I obtained an expected frequency of 17 for across-class fights using the method noted above (Appendix C).

Once, when a black vulture approached a feeding turkey vulture, they both thrust open beaks toward each other, and then, with long axes of the body dipped forward, they pushed the sides of folded wings against each other. Both birds faced the same direction, with necks lowered near the ground and heads turned off to one side away from each other. After a few seconds, they moved apart.

Differences in the degree of individual recognition may shape social relationships between the two species. Once, after a turkey vulture jumped toward an adult black vulture with an open beak, the black vulture immediately returned the attack and jumped at the turkey vulture, also with beak open. The turkey vulture repeated this pattern, and the black vulture walked away. No contact was made. In several minutes, the black vulture returned and supplanted the turkey vulture from the feeding hole by simply approaching the bird. Individual recognition seems to have been absent here. Intraspecific relations may be characterized by some degree of individual recognition, whereas across-species relations are not. This possible difference could explain why interspecific fights occurred rarely, if at all. If they functioned to establish positions in a hierarchy, even a temporary hierarchy, individual recognition would be required, or the fights would resolve only immediate conflicts and obtain less, if any, advantage for the energy spent, both for the winner and the loser.

In contrast to these findings, levels of overt aggression were reported higher in interspecific than in intraspecific relations of British titmice (Hinde 1952, p. 88), of red-winged blackbirds and common grackles (Wiens, 1965), and of black-capped and mountain chickadees (Minock, 1972). Morse (1970), however, described a reverse condition for the relationships of foraging flocks of some winter birds in North America. A number of East African vultures seem to fight more with conspecific individuals than with others (Kruuk, 1967).

Few conclusions can be drawn from these comparisons, however, because intraspecific

relations, an assumed base line in each study, may vary radically from one instance to the next. For example, relationships between members of one species may demonstrate relatively few and infrequent patterns considered aggressive, because avoidance is comparatively important in their behavior; in another species, frequent struggles might maintain strong expression of dominance.

In either case, little can be inferred about the basic characteristics shaping social organization, such as the degree of individual recognition or the degree of social experience shared by individuals. In addition, these characteristics may vary according to time and place, so that many forms of social behavior may well be similar for any given pair of species considered in comparable settings.

In sum, then, the relationship observed between these two vulture species indicated no sharp linear relation in social status. Nevertheless, several characteristic trends were evident: (1) At food turkey vultures were more retiring than black vultures; yet on a comparative basis, they dominated black vultures. This relationship is another instance linking general wariness with a dominant status (see p. 160). (2) Fighting among conspecific birds was unusually common, by *Vultur* standards, as across-class fights were rare. Fighting probably serves little purpose when the outcome of such a test does not endure beyond the period of confrontation. By this reasoning, within-species fights are more useful for either contestant, if the level of individual recognition is greater among members of one species than among those of two.

A Comparison With Old World Vultures

Old World vultures have received more attention in the field than New World species. Petirdes (1959) in Uganda and Atwell (1963) in Northern Rhodesia described interactions at food by five species. In East Africa, Kruuk (1967) made a fine quantitative study of the behavioral and ecological relations of six species; Pennycuick (1972) followed the different

species of vultures in a glider, analyzed their different adaptations for soaring, and related the differences to Kruuk's findings; and Houston (1974a, b; 1975 a, b; 1976; 1978) examined in detail food searching strategy, ecological differences among various species, and certain questions concerning breeding and food quality. Mundy and Ledger (1976) in South Africa considered the more specific but important problem of bone chips as a necessity in the diet of griffon vultures.

I briefly consider here the results of this work, the East African studies in particular. The six species of Old World vultures examined on the basis of behavior and ecology fall into three groups. The first group, comprising while-backed and Rüppell's vultures, feed mostly on dead migratory ungulates. They usually feed through holes on the carcass and take only the soft parts. Narrow skulls and beaks with trough-shaped tongues lined with horny teeth pointing rearward seem especially adapted for this type of feeding. The birds forage widely to follow the herds and may travel regularly distances of 100 km from the nest. A relatively high wing-loading ratio permits these birds to travel rapidly along thermal streets, which are long zones of rising air characteristic of these savanna habitats. No aerial pursuits or fights were seen, and the birds do not seem to be territorial. Rüppell's vultures nest in cliff colonies, and the white-backed vulture nests in trees in loose aggregations. Both species appear to rely on watching the activities of neighboring birds as their principal means of food location. White-backed vulture tend to frequent the savanna, whereas the heavier Rüppell's vultures concentrate in the highlands, where deflection currents can substitute for thermals during periods of heavy cloud cover.

The second group, composing lappet-faced and white-headed vultures, have broad skulls and thick beaks, apparent adaptations for tearing strips of meat and skin off bones. Both are also known to kill their own prey. The two species seem to have their own home ranges and may be territorial; intraspecific aerial disputes were observed. They probably tend to locate food

directly, instead of following the activities of neighboring birds. Relatively low wing loading ratios permit flight in poorer thermal conditions but at slower speeds. Cross-country flights by these two species were not seen. Both species nest in three and are solitary nesters. The aggressive lappet-faced vultures usually feed among griffon vultures on animals dead from disease or malnutrition, whereas the comparatively timid white-headed vulture tends to feed alone on smaller carcasses that are often predator kills.

Hooded and Egyptian vultures are the smallest of the six and represent the third group. These species tend to feed at the fringe of activity at the carcass, where they pick up bits from bones and the ground. Both also feed on insects and garbage and are common around human habituation. Hooded vultures are solitary nesters and use trees, whereas Egyptian vultures nest in cliffs and are usually solitary. Hooded vultures frequent the savanna and forest; Egyptian vultures are found in drier country.

In a number of comparisons differences that are marked among African scavengers are blurred among their New World counterparts. Andean condors have trough-shaped tongues with horny teeth and feed on soft parts, as do members of the first group of African vultures. However, they also tear meat and skin from bones like the second group and may be predatory. Black and turkey vultures frequent human habitations like Egyptian and hooded vultures, but they also feed directly on carcasses and kill at times.

New World vultures do not seem as specific in nest preferences as the Old World species. I saw only two occupied Andean condor nests, but both were in the same area at different periods, and both were in the vicinity of roosts used by other adult pairs. In Argentina, I was told of several "*buitreras*" where condors congregated and may have nested; nest aggregations may have occurred in earlier times when condors were more common. Cole (1938, p. 262, 267) discussed reports of gregarious nesting in the turkey vulture, a cathartid, considered today as a

solitary nester. Black vultures using eroded caves in cliff faces sometimes nest in aggregations (Brown and Amadon, 1968). California condors typically nest in cliffs, but one instance of tree nesting was reported by Koford (1953:81). Turkey vultures nest in trees and cliffs, occasionally on the ground, in abandoned buildings, or in hollow logs (Coles, 1938, p. 251). Black vultures also nest in trees and cliffs, on the ground, in both abandoned and occupied buildings, or in the nests of other birds (Steward, 1974; Brown and Amadon, 1968). Nests of the king vulture, a bird of the tropical forests, have been found on the ground and in stumps near the ground (Smith, 1970). Andean condors might also use trees in the southern part of their range where large trees still exist. Nest selection in general, then, seems relatively more flexible among New World species.

In Colombia, the resident populations of condors appeared to have fixed foraging routes. Territoriality was probable, with aerial pursuits common. These conditions resemble those of the second group of Old World vultures in East Africa. In Paracas, however, condors often roosted, flew, and fed together in large groups and behaved more like the first category of Old World vultures.

In some comparisons, the differences between Old and New World species were not so blurred. In East Africa, a definite order of arrival seemed based on foraging strategy. Species arriving at first tended to be those that foraged over home ranges seeking food, whereas vultures that followed the movements of neighbors usually followed quickly. The smaller turkey or black vultures usually preceded condors at the baits in this study, but the order of arrival likely depended on different factors. In Africa, vultures must compete with mammalian scavengers so an early arrival is imperative for securing food. In South America, mammalian competitors play a minimal role, so that the major risk in the approach of condors is the proximity of man. Turkey and black vultures are less wary than condors and this fact, more than any other, probably

determined the order of arrival observed in this study.

Size apparently determines the interspecific hierarchy observed for birds both in Africa and in this study. Dominant species in Africa were the Rüppell's and lappet-faced vultures, the two largest species, and in this study condors were dominant over smaller vultures. Although other factors like thermoregulation, the regular availability of food, and flight must be important influences in the evolution of size, this relationship with interspecific dominance must play a role, and probably a larger one in Africa, where diversity among scavengers is greater and the gradations of difference among them are fewer.

The African savanna supports the largest biomass of living animals on land, represented mostly by migratory ungulates. This extreme condition is probably the major reason why twice as many species of avian scavengers live there than in the South American areas of this study. Using estimated amounts of food available for scavengers in the Serengeti region of East Africa by Houston (pers. comm.), I calculated an average value of 700 to 3200 kg per km^2 each year, compared to a similar estimate of 200 kg per km^2 in the Paracas study area (raw data from Tables 49 and 50 extrapolated for a study area of 500 km^2). Although these estimates are crude, the difference (3.5 to 16 times as great in Africa) indicates a substantial difference in food availability between the two ecosystems. In addition, thermal conditions over the savanna are probably more conducive to long-range cross-country flights, making possible a diversity of avian scavengers, some the travel long distances and others that remain in a relatively smaller area. Thermal streets are not common, if present at all, in the mountains and coastal habitats examined in this study. African vultures flew long distances for food (white-backed vultures at least 80 km, Rüppell's 150 km; Houston, 1976) and normally visited their nest only once a day, whereas Andean condors visited their nest an average of three times daily. These condors foraged over a comparatively smaller area. The smaller black and turkey vultures with lower

wing loading ratios probably do not forage over areas any larger than those of the condor.

In general then, a larger and more diverse amount of available food and the wider range of flight possibilities allow for larger scavenger populations in Africa than in the areas observed in this study. Diversity among the different species in Africa may reflect a selection for character displacement where species with similar requirements overlap; greater feeding and foraging specialization would reduce interspecific competition. Kruuk (1967) noted that whenever the foods of two African species are similar, overlap of their geographical ranges is relatively small. The diversity of avian scavengers in East Africa, reflected by the overlap of all these ranges, is not surprising when one considers the prime conditions there for feeding and flight.

In sum, the three New World vultures examined in the study seem broader in nesting, feeding, and flight requirements than the six species of Old World vultures in East Africa. These generalist tendencies of the New World species probably stem in part from the relatively smaller amount of available food and more limited flight conditions.

RELATIONSHIPS WITH OTHER BIRDS

Black Chested Buzzard-Eagles

The black-chested buzzard-eagle is an aggressive raptor with a shape and flight similar to that of the *Buteo* hawks, although the buzzard-eagle is somewhat larger. According to Colombian *campesinos*, buzzard-eagles frequently take domestic chickens and turkeys. I saw one bird capture a black vulture after a prolonged and spectacular pursuit in flight. Relationships observed between buzzard-eagles and condors usually involved aerial pursuits. On 15 separate occasions, I saw buzzard-eagles, both adult and immature birds, dive at and pursue condors. The chased male and female, immature and adult condors. Most of these pursuits were single dives;

the buzzard-eagles dropped with half-flexed still wings at glide angles ranging from 45^{o} to nearly 90^{o}. Except for one instance, when an adult male was truck on the back while watching me as he glided by, the condors successfully evaded contact by diving with flexed wings and by weaving from side to side. Most of the buzzard-eagles came within about 30 cm of striking the big vultures, although a few approached no closer than about 10 m. In three of these instances, the buzzard-eagle dove down upon the condor three times in succession. Usually, the pursuing buzzard-eagles screamed repeatedly while giving chase. They dove from altitudes 10 to 30 m above the condors. Evasive descents by the condor were usually no more than 50 m, although one immature male dropped about 100 m, with the buzzard-eagle closely behind. Sometimes the pursuits ceased when the condors landed, although I once saw a buzzard-eagle dive at pair 1 when they perched at their bathing site in the roost area. The condors did not fly, and the buzzard-eagle left after circling six times about 7 m above their heads. After diving upon condors, buzzard-eagles rarely followed them more than 50 m. Except for one pursuit observed in the Paracas area, all chases were seen in Colombia. Four of the pursuits observed occurred in the roost area of pairs 1 and 2 during one 10-week period; perhaps the buzzard-eagles had just begun to nest.

Pursuits in the reverse context might also function in protecting the nest. On six occasions, we saw condors, all nesting birds, dive upon and pursue flying buzzard-eagles. Four instances involved AM2, and the other two were by AF2 and AFA. All incidents occurred in an area less than 200 m from the nest on the bird in pursuit. Flight of the chasing condor ranged from a nearly vertical dive of 25 m with wings less than half extended to a nearly level, weaving, gliding pattern with feet lowered and wings flexed. The extent of five pursuits was no more than a single dive by the condor, each of which seemed to be easily avoided by the buzzard-eagle. Usually, just before the condor was within 1 m, the buzzard-eagle shot off to one side descending

at an angle of about 30^{o} with the horizontal. Dropping about 10 m each time, AF2 dove twice at one buzzard-eagle. Koford (1953, pp. 64, 126) saw California condors both in pursuit of and pursued by golden eagles in one observation an eagle struck a condor with its talons.

At the baits in Colombia, visiting buzzard-eagles had a marked effect on the feeding activity of both black vultures and condors. One about one of every three days at the bait, a buzzard-eagle soared overhead, and the black vultures rushed to huddle in a mass over the carcass. After the eagle passed overhead, separate flocks of black vultures took off irregularly until, in many instances, all of them were airborne. Any condors present when the vultures rushed together usually took off immediately. Once, the huddled vultures all took off together when a buzzard-eagle, gliding over the canyon, suddenly dove down upon a red-backed buzzard flying below it.

Other Birds

Condors were pursued in the air by both kelp and Peruvian gulls. Although the gulls dove very near to the flying condors, I never saw them make contact. Most of these observations were made at Isla Zárate where, apparently, condors were being driven from gull nesting areas. Once, three gulls attacked two adult female condors perched near the top of a cliff on the island. The gulls dove at them repeatedly, until they took off. The pursuits continued in the air, and the condors descended steeply, weaving from one side to the other. The condors landed on a ledge below and then ducked their heads many times as the gulls continued flying at them for several minutes. Four gulls attacked another adult female feeding on the beach. She dodged them for several minutes but finally ran, took off, and flew to the other end of the island. The gulls did not follow. Many of the aerial pursuits involved only one gull and one condor. Sometimes the condor flapped rapidly while remaining in level flight, and other times the condor and gull

descended in rapid and twisting gliding patterns. At the carcasses, both condors and turkey vultures alike supplanted both species of gull. Sometimes perched condors became alert and extended their necks and turned their heads when gulls cried out.

Infrequently, in the Colombia study area, the crested caracara chased condors and black vultures in the air. In one pursuit, a caracara dove several times at an adult female condor before finally striking the big bird on the back once with its feet. I saw no interactions between caracaras and condors at the bait. On several occasions, however, I did see black vultures and caracaras involved in social preening patterns. One caracara approached four black vultures in succession and extended his downward-pointing head toward each of them; each vulture preened feathers on the back of the caracara's head for 2 to 10 seconds. Later, this caracara chased a black vulture in flight.

In the Cerro Illescas, I saw an osprey pursue in flight an adult female and a sub-adult female condor. The osprey called out several times. All birds flapped in level flight after the osprey dove at the condors. In the Paracas area, an osprey dove four times at an adult female condor flapping in level flight along the coast. In all instances, the osprey came within about 1 m of striking the condors.

RELATIONSHIPS WITH MAMMALS

Sea Lions

Approximately 1000 sea lions lay on the beaches of Isla Zárate during the October to February period when we watched condors there. Apparent interactions between the two species were infrequent and usually occurred only when condors sought food near the mammals. In general, younger, smaller lions moved away from approaching condors, and condors often ran from adult sea lions that shuffled toward them. Sometimes the smaller mammals moved toward

the sea whenever adult condors approached to within 10 to 20 m, although occasionally condors walked by or fed near sea lions only 3 to 6 m away, and I could see no apparent reaction by members of either species to the other. Responses often seemed related to the speed of movement. When condors ran near sea lions, the mammals usually moved toward the water, and when a sea lion lumbered after a condor, the condor ran, usually with wings extended. I saw an adult female condor jump back when a small sea lion, probably a yearling, hobbled by her quickly.

Most of the prolonged encounters between sea lion and condor occurred when a condor attempted to pull a small carcass away from a group of sea lions. Occasionally, condors persisted in returning to areas they had been chased from by sea lions. One adult male condor was pursued 21 times before he finally retrieved a dead pup. On another occasion, a sea lion retrieved a dead pup from an adult condor that had dragged it 7 m off to one side and fed on it for 30 seconds. The sea lion carried the dead animal back in its jaws, dropped it and lay down beside it. After a few minutes the sea lion finally moved away from the pup, and a condor pulled the small animal about 15 m away and fed on it.

We saw ten other similar instances where sea lions repeatedly chased condors attempting to pull out a small carcass. In most cases, the condors persisted in their attempt and were able to move the carcass far enough from the sea lion to feed. In seven of these cases, the pursuing sea lions were large bulls. Occasionally, condors were observed to peck at and pursue live young sea lions; I describe these observations in the section on predatory behavior in chapter 7.

Response to Humans

Although condors frequently flew near exposed humans, they rarely landed or remained perched when humans appeared. When we visited roosts in the Paracas area and exposed

ourselves within 100 m of the perched birds, many took off immediately; some extended their necks and watched us carefully. Those remaining on the cliffside always flew within moments after we moved from their sight. If we made any sharp movements or shouted, perched birds took off instantly. Condors frightened from a roost did not return there again that evening. Rarely did condors feed when humans were visible within 1 km.

Aerial Scrutiny.

In all three study areas flying condors frequently approached us and watched us closely while circling overhead, usually less than 100 m away (Plate 27). Durations recorded for 20 of these aerial patterns ranged from 5 seconds to 4 minutes with a median of 1 minute. In the brief patterns, condors veered from a straight course, glided above us, and turned back to the original flight path. Two-thirds of 71 patterns of aerial scrutiny recorded were by adult males (Table 39). Immature birds, particularly males, did not approach as often; part of this difference can probably be attributed to fewer observations of immature birds in flight. For adult birds, the pattern was clearly associated with males, becausee adult of both sexes were observed in flight at equivalent frequencies. In the Cerro Illescas, an area where humans were rarely seen, condors that approached and circled above us sometimes alighted two or three times on a hilltop less than 500 m from us. The perched birds continued to watch us alertly.

At the Nest.

Nesting birds appear sensitive to human intrusion. Both nests found in Colombia resided in an area not often frequented by people. About twice a month, one or two men traveled to the river below the nest cliffs to look after cattle that grazed there. Sometimes nesting adults circled near these men when they appeared in the nest vicinity. Once, AF2 ran out from the nest cave when a gunshot sounded in the canyon; she looked about for 15 to 20 seconds before turning back to the cave.

Plate 27. An adult female watching the photographer while circling overhead. Note the fluttering coverts on the leading edge of the wing and the white stains of excreted material deposited on the tarsus.

Table 39. Aerial scrutiny of humans. A tally of occurrences for circling flight patterns by condors within 100 m of fully exposed humans.

Study area	Percent of occurrences by sex and age class: Adult male	Adult female	Immature male	Immature female	Total no. observations
Colombia	78	22	0	0	18
Paracas	71	17	0	12	24
Cerro Illescas	55	31	0	14	29

When I first approached to within 200 m of the nest, AF2 circled nearby and watched me closely. Then she landed on the nest cliff and watched. AM2 landed beside the chick and fed him while I stood in full view. He may not have seen me until after the feeding; then he watched closely with neck extended toward me. When I returned the next day and constructed a blind about 150 m from the nest, both adults stood on the nest cliff less than 20 m from the chick and watched me for the full 65 minutes that I was present there. Either bird could have been shot easily.

After watching the nest and chick from the blind for three days, I climbed down to the chick to weigh and measure him. The adults did not appear. On the following day, I watched the nest from the blind to confirm that the parents were still caring for the nestling. AM2 went to the nest and fed the chick in the morning. Three days later, however, when I watched the nest from across the canyon—at our usual viewing station—neither parent appeared the entire day. This was the first occurrence of such an absence. I feared that the chick had been abandoned so I returned the following day and took the young bird. Yet, two days later when I returned to the nest area, I saw AM2 and AF2 land together at the nest cave for 15 minutes and then fly from the area. My presence in the immediate vicinity of the nest area seemed to have affected their relationship to the nest and young, although it might not have caused abandonment. Koford (1953, p. 98) reported similar effects of his presence on nesting California condors. In a demographic study of the California condor, Mertz (1971) demonstrated mathematically how "individual fitnesses would be higher if increased in mortality were absorbed by the preadult rather than the adult component of the population;" he noted that this relationship might account for the marked sensitivity of adult condors to nest disturbance. The apparent effects of human intrusion on parent-young relationships indicate that proper management of both species of condor should include the preservation of nesting sanctuaries that humans do not enter.

Other effects of man on Andean condor mortality are considered in Chapter 9.

Other Mammals

In Colombia, cows, horses, and dogs occasionally visited the baits when condors were present. In all instances, the condors seemed alert to their presence and avoided being in close proximity with them. An adult female left the bait, walked 10 m uphill and waited for 5 minutes when 10 cows approached. After the cattle left, she returned and fed. On another occasion, an adult female landed when several cattle stood near the bait. She walked down the hill, circled the cattle and the bait, and returned to the upper slope above them. When the cattle walked to within 2 m of her, she flew. On two separate occasions, an adult male feeding at the bait took off when approximately 20 cows grazed to within about 20 m of him. IM2 flew from the bait when several horses rattled the brush in a thicket 200 m away. When a small dog, approximately 10 kg in weight, approached the bait, all the condors and black vultures present took off. Several individual flocks of black vultures departed before the condors, two adult females and one adult male, left. About 200 black vultures were present. On another occasion, an immature male and immature female condor left the bait and stood on the canyon rim about 80 m away when a dog came and fed. Neither bird flew, even when I yelled at the dog from the blind; they did not return to feed that day, however.

CONCLUSIONS

Condors, black and turkey vultures sometimes perched near each other and occasionally were seen flying together. Most of their relationhipss, however, occurred at the food items that they shared. Both black vultures and turkey vultures seemed drawn to condors, probably because the pressure of condors often indicated food.

The large condors were clearly dominant over their smaller counterparts. Turkey

vultures usually moved from the area where condors fed, whereas black vultures often fed together in the same sites on the carcass. Adult condors, particularly females, supplanted neighboring black vultures more actively than did immature condors, with average rates ranging from 3.5 displacements per minute for adult females to 0.8 per minute for immature males. In Colombia, black vultures bit at and pulled feathers of feeding condors at an average rate of 0.5 occurrences per condor minutes when condors were feeding. Condors reacted to this apparent form of harassment by turning, biting, and chasing nearby black vultures, often non-offenders. Condors can tear holes in the hide of cow and horses, but black vultures cannot. Smaller vultures can feed in newly opened areas if harassed condors depart from the baits earlier than they would otherwise. Harassment seemed effective, not as a direct threat of harm, but as further inducement for flight by a bird usually sensitive to any confusion.

In the Cerro Illescas, I saw no instances of this harassment; condors seemed much less wary in this Peruvian area and harassment may not have been as effective here. Possibly, the harassment behavior is specific to certain populations of black vultures where condors are shot at and, as a consequence, are more alert and wary. Marked differences in alertness by condors were, indeed, locality-related (see the section on alertness in the chapter on feeding behavior). Black vultures were supplanted by condors at lower rates in the Cerro Illescas than in Colombia, perhaps as a result of this difference in aggressiveness by the smaller birds.

The general direction of supplanting patterns between the two species indicates that turkey vultures tend to dominate the black vulture. Within-species fights were common among the two species of vulture but across-species fights occurred only rarely, if at all. If birds are unable to identify individuals of the other species, fights would serve only an immediate purpose and would not contribute to any established hierarchy. Such a short-term gain might not be worth the energy loss and potential danger of a fight. Also, potential contestants of different

species may not be able to judge accurately the likelihood of winning such a struggle.

Relationships between condors and other birds were usually restricted to aerial pursuits. Pursuits between condor and black-chested buzzard-eagles may have been related to the proximity of a nest belonging to either bird. Condors frequently flew from carcasses when black vultures rushed to huddle after a buzzard-eagle passed nearby.

In this study, the only mammals with any notable relation to *Vultur* were sea lions and, of course, man. Sea lions frequently pursued condors feeding near them. Occasionally, condors pecked at small live sea lions. At times, the vultures were notably tenacious in their efforts to extract the dead young out of the midst of a group of sea lions. Typically, condors avoided humans and, as a rule, did not land in the presence of any person. On many occasions, however, condors, particularly adult males, flew near exposed humans, circled around, and watched them carefully for about 1 minute before soaring away again. Nesting condors seem particularly sensitive to the presence of humans and may abandon nests if disturbed.

Whereas three species of New World vulture may feed together in South America, six species of vultures often frequent carcasses in East Africa. Food is available in much larger quantities in these African area. Thermal conditions in the Africa savanna probably allow larger and more rapid cross-country flights by avian scavengers than those in the South American areas that we frequented. Both conditions in Africa probably encourage relatively larger scavenger populations, with more specialization in feeding and foraging techniques. In a number of comparisons of feeding, foraging, and nesting activities, the three species of New World vultures seemed more generalized than their African counterparts.

CHAPTER 7 FEEDING

INTRODUCTION

We watched condors feed from blinds and baits in all three study areas. We also observed feeding condors across a channel on a small island, Isla Zárate, near Paracas on a mainland point. Objectives in the study of feeding behavior included a determination of food preference, feeding timetables, and methods of food location, and an examination of age, sexual, and population differences in feeding techniques.

In the first part of this chapter, the condor's food is described and preferences examined. Some information on food preference came from providing a variety of baits at the blinds. In one analysis of scavenger food preference, I calculated, for each food species, the amount consumed as a percentage of that available, and ranked preference according to the proportion consumed.

The next section of this chapter considers how condors locate food, arrive and depart, durations of feeding bouts and visits, and where and how they feed. Age-or-sex-specific techniques or preferences are examined. Alertness at food is considered according to the sex and age of the bird and location of the food item. I made some comparisons with other scavengers.

The last section deals with the feeding ecology of avian scavengers in one community. The Paracas area was an excellent location for such a study. Except for an occasional desert fox, few animals ever wandered or flew back in the desert away from the beaches. Because vultures are unable to take food from the water, the food available to them was concentrated in a thin band along the coast. This nearly linear distribution of food for scavengers provided an ideal situation to examine the interrelations of the food supply and avian scavengers of that area:

condors, turkey vultures, and gulls. I included two species of gulls, the kelp gull and the Peruvian gull were considered here because they frequently fed on the same animals as vultures.

The study attempted to answer three general questions: (1) How much carrion food mass was available on the beach stratum of the coast community, and how much was consumed by avian scavengers? (2) how was food partitioned among the different species of avian scavengers? and (3) how did the distribution and size of condor populations reflect the distribution and amount of food?

FOOD

Kinds of Food

In Colombia, baits included adult cows, horses, and burros, as well as colts and calves. We also saw condors feeding upon dead mules and goats that had fallen into the Rio Pasto and Rio Juanambú canyons. During the dry seasons of the northern summer and winter, domestic animals fell into the canyons while trying to reach untouched grasses low on the rim. In the wet spring and fall, they often fell after slipping from the muddy trails.

On the Peruvian coast, wild animals composed most of the condors' food. At Paracas, I saw condors feed on dead sea lions, fur seals, Burmeister's porpoises, Humboldt penguins, Peruvian boobies, guanay cormorants, brown pelicans, and sharks. On the rocky beaches of Isla Zárate, they sometimes fed on scattered chunks of flesh that appeared to be the placentas of sea lions. Murphy (1925, pp. 190-191) reported that the stomach contents of three condors taken on the southern coast of Peru contained a hoof and a few bristles of a domestic pig, two leg bones and some cartilage of a fur seal, parts of a Humboldt penguin and a Peruvian diving petrel, bits

of kelp, fish scales, and pebbles. He also reported predation on eggs of the guanay cormorant. In the Cerro Illescas, condors that visited the baits fed on burros and fur seals. A goatherder living there claimed condors killed many of his newborn goats every June. Feral goats and burros as well as sea birds on the coast probably represented a major part of the food of this population.

Preferences

Condors frequently demonstrated food preferences. In Colombia, I saw AM1 pull several meters of intestine from a horse and then leave it to the black vultures, while he fed and red muscle farther inside the hole he had made. The captive immature condor was notably selective, preferring meat that was (1) fresh rather than sour, (2) moist rather than dry, and (3) firm and fibrous rather than soft and flaccid. During some periods, he fed selectively on the fat and avoided lean parts. In contrast, an adult female that I watched feeding in the zoo at La Paz, Bolivia, selectively consumed the lean part of the meat she was given and left the fat. Variations in preference may be related to certain deficiencies in the diet.

In the Paracas area, a variety of food was often available in the same area at the same time, so preferences in the type of food species chosen were apparent immediately. Condors as well as other avian scavengers appeared to favor birds more than mammals, reptiles, or fish. In a preference ranking for avian scavengers obtained by computing for each food species the percent eaten of that available, values ranged from 72.3 percent for the Humboldt penguin to 0.3 percent for decomposed sea lion (Table 54). A category of other birds followed the penguin in this measure of preference, and brown pelicans and guanay cormoran**ts** represented third and fourth

positions.

At one blind, where parts of a horse, a decomposed fur seal, and a pelican served as bait, two condors and a few turkey vultures fed only on the pelican. At another blind where a 15 kg dogfish and a pelican served as bait, two condors and a few turkey vultures fed only on the pelican. At another blind, where a 15-kg dogfish and a pelican served as bait, an adult male condor fed on the pelican for 20 minutes and then nibbled briefly at the mouth of the shark before leaving. Only about 200 g of flesh remained on the pelican when an immature female condor landed. She fed on the remainder of the pelican for 10 minutes, nibbled at the shark briefly, and then returned to feed on the pelican for another 5 min. She consumed the entire gular pouch and all of the skin between the toes of the pelican but took little of any from the shark. The eyes and intestines of the shark were eaten by an adult and immature female condor, but the muscle was left untouched.

Although black and turkey vultures have been observed catching and eating fish (Jackson *et al*, 1978), condors seemed to avoid them. I never saw a wild condor eat the muscle of any fish; the captive immature condor refused all fish that he was offered.

The flesh of porpoises also appeared to be of low preference. An adult female landed near one blind baited with a porpoise and fed instead on the old, dry remains of a Peruvian booby. Although an adult male and female fed on the two sea lion carcasses at another blind, they did not touch the fresh carcass of a porpoise lying there. When they did feed on porpoises, condors sometimes took only the skin and the shallow layer of flesh and fat beneath. On a single visit, an adult female ate about one-fifth of the entire skin of a medium-sized porpoise. She, too, ate most of the skin on the belly of the animal. On another occasion, condors took only the belly

skin and viscera (Plate 19). According to Koford (1953, pp. 55-56), California condors prefer the carcasses of deer and young calves over those of horses, mules, and coyotes.

FEEDING BEHAVIOR

Locating Food

In Colombia and in the Cerro Illescas, condors seemed to locate food by flying over large areas. On a few occasions in Colombia, I was able to follow the movements of birds that were apparently foraging. One condor circled in an area 1-km square for 25 minutes. Another adult aloft for one hour remained in a rectangular area of 6 by 20 km; eight circling ascents separated long intervals of flex-gliding. At an average air speed of 15 m/seconds, this condor would have traveled an air distance of 54 km. Several of the flight paths left the same origin and crossed to nearly the same endpoint. Nevertheless, they traversed country of sharp relief at different altitudes, thus obtaining different views of the canyons and ridges below. An adult male apparently foraging in one centralized area was visible for 4.5 hrs (Table 40); almost two-thirds of this time was spent in flight, and all within a rectangle 6 by 8 km. Assuming an air speed of 15 m/sec, I estimated that this condor covered an air distance of 156 km. In circling, however, most of the air distance was confined to one area on the ground. By considering only the gliding time (97 minutes, 36 percent of time observed) and neglecting any wind effect, I calculated that the ground distance covered was 87 km. The flight paths of this condor seemed unusually restricted and should not be considered as typical foraging activity. Rarely could I follow the activities of flying condors for more than 30 minutes.

It is unlikely that all flights serve in the search for food. One afternoon, I watched AM1

Table 40. Activity of an adult male condor in the Colombia study area on 17 January 1968 from 1130 to 1600.

Activity	Time spent in each activity to nearest min – listed in order of occurrence –>	Total	Percent
Flight:			
Gliding	10 - 5 - 4 - 4 - 1 - 2 - 1 - 2 - 1 - 7 - 2 - 14 - 9 - 2 - 3 - 3 - 3 - 3 - 6 - 2 - 1 - 12	97	36
Circling	10 - 5 - 4 - 3 - 3 - 4 - 2 - 5 - 10 - 1 - 3 - 3 - 7 - 2 - 2 - 4 - 6	74	27
Flapping	2	2	1
Perched:			
Motionless	18 - 1 - 11	30	11
Preening	15 - 5 - 7 - 4 - 13 - 9 - 12	65	24
Sunning	2	2	1

fly and perch repeatedly in the immediate area of the roost for 135 minutes. Over 40 percent of this time was spent in 12 bouts of flying, yet all of the flight paths were confined to an area of about 0.25 square km. Foraging flights are probably not so limited. Perhaps these instances of restricted flight paths function to cool the bird (see p. 66).

In the Paracas study area, condors followed the coastline in linear routes of foraging. Several observations there suggested, however, that food location involved more than a simple search-and-find method. In January 1969, over a 3-day period, I noted a steady increase in the numbers of both sea lions and condors on Isla Zárate, yet during the same time, biomass available for scavengers diminished. The condors may have been following the coastal migration of live sea lions, or they may have been responding to some other proximate factor like seasonal changes. Perhaps the onset of this annual migration is associated with periodic food abundance of a particular season.

At times, condors apparently followed the activities of a foraging neighbor, either to locate food or to confirm the safety of feeding there. At Playa Chucho, I saw at least 18 different condors alight at a sea lion carcass one morning before 0915. The carcass had been lying in the same position for 8 days, yet condors had not alighted earlier. As noted before (p. 119-122), the presence of one condor at the bait seems to facilitate the arrival of another, so the sudden appearance of a group was not unusual. The size of the group, however, was. During the preceding nine days, an average of five condors crossed that beach during the period from daylight to 0915. Numbers ranged from 1 to 13. The larger size of the group on that one morning ($\geq$18 birds) suggests that some of the birds sensed the food and, perhaps, the safety of feeding assured by the presence of others, all without actually seeing the carcass or the other

condors alighting beside it.

In this area, condors were apparently unable to ascend above altitudes much higher than the sea cliffs (see Chapter 8), so they would be unable to note any activity from high-altitude positions at distant locations. Perhaps condors periodically note the activity of foraging neighbors and then tend to fly in the direction of those that move from view. In this way, the foraging advantage of a single bird would be multiplied by the number of other condors monitored. One function ascribed to social roosts is that they serve as information centers for finding food (Ward and Zahavi, 1973, p. 173). In departing from the roost, birds may lead one another to food located the previous day.

Other scavenger species might be watched as well. Most of the feeding activity by condors observed on the coast involved groups of condors, turkey vultures, and gulls, although a few condors landed and fed when other birds were absent. Observation success at the blinds appeared to increase when I slit the skin of the baits exposing the flesh. Turkey vultures and gulls arrived in larger numbers and fed more actively. Both conditions appeared to attract condors. In East Africa, Houston (1974a) found that griffon vultures often located food by following the activities of a neighboring bird. Kruuk (1967) reported that lappet-faced vultures arrived first at carcasses in numbers greater than that expected on the basis of the proportion of this species in the scavenger populations there; he cited this phenomenon as evidence that these vultures tend to look for food directly more than griffon vultures do.

The senseof hearing may occasionally figure in the location of food by condors, whereas smell seems of little importance. Rodolfo Scaiola, a stockman of Mendoza, Argentina, told me that condors there were attracted by the sounds of gunshot; the birds likely associated the sound

with the appearance of viscera from the animals shot and gutted there. Davis (1979) cited an instance of five turkey vultures appearing within 1-2 minutes over an area where shots had just been fired. Although turkey vultures and, possibly, king vultures use smell to locate food, the olfactory morphology of both *Vultur* and *Gymnogyps* suggests that this modality plays only a minor role, if any, in food location (Stager, 1964, 1967). I found no field evidence for food location by smell with *Vultur*.

Locations Used

In Colombia, condors visited the baits I placed on the canyon rim. Other feeding went on inside the canyon. Condors fed on one steer that had died in a gully near the river. The narrow ravine, about 10 m in depth, was accessible to man from below. Condors feeding there had only a limited view, yet an adult male fed for 15 minutes and an immature male for 32 minutes. In a brushy area near the top of one ridge, I saw an adult pair feed on a dead goat. The brush was about 2 m high and covered about 70 percent of the area to present somewhat unusual conditions for take off and landing. In the Cerro Illescas, condors foraged and fed throughout the mountains, along the coast, and even out onto the desert plain of Sechura. I saw adults circling over the plain 65 km from the nearest roosting area.

In southern Peru on the coast, most, if not all, feeding was restricted to the water's edge, on beaches, and at bases of sea cliffs where the bodies of dead or dying animals washed ashore. Usually, these condors made little apparent response to the sound and motion of the surf. I saw water momentarily cover the feet of one adult female. She had dragged part of a bait down the beach toward the water. After the water touched her, she began pulling the animal parallel to the

line of surf. An immature female approached this bait later but moved back repeatedly when the surf came in. Finally, she left after approaching only to within 2 m of it. On Isla Zárate, I saw an adult female feed on a sea lion about 1 m back inside a cave. The cave entrance was about 3 m high and 1 m wide. Just 400 m from the Pan-American Highway south of Chala, Peru, I watched six adult condors feeding on a dead sea lion. Three other adults and one immature condor circled overhead. On Playa Chucho, while I stood in full view, an adult female landed 250 m from me and fed on a pelican. First, she picked it up and carried it several meters away from me. She fed for 10 minutes before flying. Another adult female fed on a Peruvian booby after we drove to within 1 km of her. She carried the bird 5 m up the side of a hill and resumed feeding for 10 minutes. The additional altitude would have facilitated a quick take-off.

Periods of Feeding

In Colombia, condors tended to feed during the middle of the day; 61 percent of the condor minutes recorded at baits occurred during a 3-hour period from 1000 to 1300. Time spent at the bait by condors increased sharply at 1000 and tapered off gradually after 1300 (Table 41, Figure 28). Sex and age-class differences in preferred hours of feeding were not apparent. Although condors rarely sought and found food before 1000 in the Colombian study area, the crops of many birds in the Paracas area were rapidly being filled before this time. Daily winds necessary for flight came up earlier in the Paracas area.

Using records on the size of crops observed in the field, together with data relating crop size and food mass consumed by a captive condor, I estimated the mean mass of food carried per condor during each of seven 2-hour periods (Table 42). The largest increase in crop contents

Table 41. Bait visitation in Colombia and the time of day. Data recorded during 60 days of observation from 1 October 1968 to 15 March 1969.

	No. visits	No. visit. min	Percent by time of day										
			0800-0859	0900-0959	1000-1059	1100-1159	1200-1259	1300-1359	1400-1459	1500-1559	1600-1659	1700-1759	1800-1859
Adult male	167		1	4	16	22	19	13	11	8	4	2	2
Adult female	145		1	7	11	17	20	12	13	8	4	6	2
Immature male	155		0	6	10	27	25	17	9	3	2	2	0
Immature female	21		0	5	19	19	29	10	10	10	0	0	0
Adult male		1068	1	6	21	21	11	12	11	5	5	3	5
Adult female		1269	1	8	19	15	15	13	11	5	6	4	4
Immature male		3420	0	3	26	20	21	15	8	3	3	2	0
Immature female		542	0	1	21	20	24	10	6	7	10	0	0

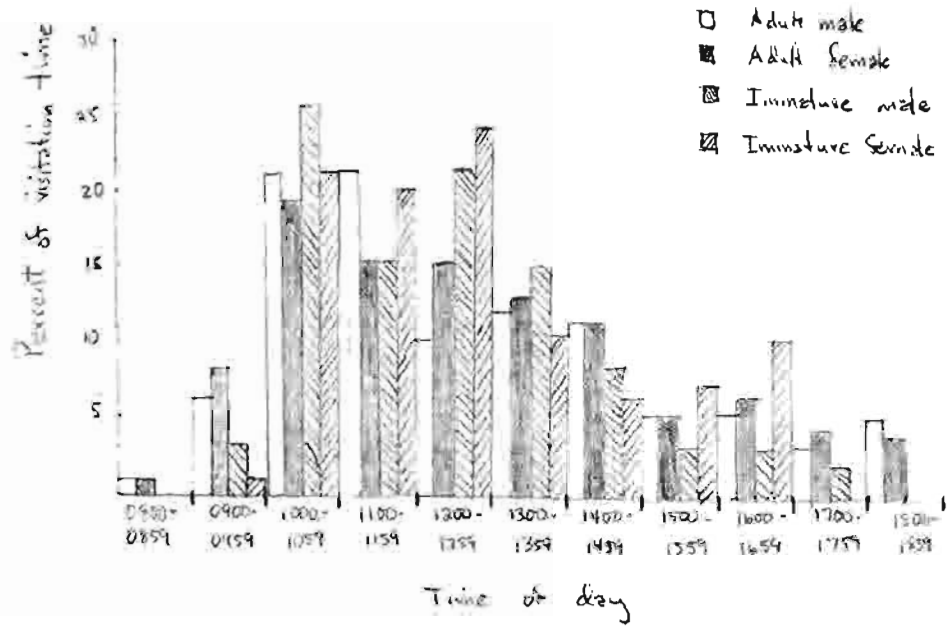


Figure 28. Bait visitation time in Colombia and the hour of the day. Data from Table 41

Table 42. Crop size of condors in the Paracas study area at different times of the day. Data recorded from April 1969 to February 1970.

Time of day	0500-0659	0700-0859	0900-1059	1100-1259	1300-1459	1500-1659	1700-1859
No. of observations	27	110	324	161	151	80	86
Percent of observations by crop size observed in field[a]							
Stage 1 (0-80 g)	93	68	65	68	56	44	66
Stage 2 (81-200 g)	0	8	3	4	2	10	10
Stage 3 (201-300 g)	0	0	1	3	1	6	0
Stage 4 (301-400 g)	4	5	6	1	7	6	7
Stage 5 (401-500 g)	0	6	4	4	7	6	2
Stage 6 (501-700 g)	0	3	2	1	5	9	5
Stage 7 (701-800 g)	0	0	2	2	1	0	1
Stage 8 (801-1500 g)	4	10	18	16	21	19	8
Mean mass (g) of food	56	187	274	242	334	348	180

[a] Food-mass estimates obtained by recording values for food consumed by a captive male.

computed for consecutive periods occurred during periods preceding and following 0700 (56, 187, and 274g), indicating that a major period of daily feeding occurred about that time. A sharp drop in mean values at 1700 (348 to 180g) suggests that little or no feeding took place after this afternoon hour.

I did not test for differences in the hourly distribution of condor minutes at Colombian baits or of arrival occurrences. Units were not independent in either measure. In the latter instance, arrivals were often clustered, because birds tended to take off and land repeatedly when they were in the bait area. Data on the crop size of Paracas condors were independent, however, and I tested for differences according to the time of day (with a chi-square test on the raw data used to prepare Table 42). Stages 2 through 7 on crop size were combined in this test (81 to 800g). Differences were highly significant.[1] In the notable deviations, empty crops were observed more often than expected from 0500 to 0700 and less often from 1500 to 1700. Full crops were seen less often than expected from 0500 to 0700 and more often from 1300 to 1500.

Approaching Food

Most of the condors visiting the bait in Colombia circled overhead, landed on the hillside above, and then walked hesitantly down to it. Slightly more than half of 39 landing sites recorded were less than 3 m from the bait; 18 percent were greater than 10 m (Table 43). Differences in recorded distances between landing site and bait seemed unrelated to sex and age of the bird. About 75 percent of the landing sites were above the carcass. After alighting, condors usually stood and looked about for periods ranging from a few seconds to several minutes and then , pausing frequently, walked toward the carcass. In general, immature birds

Table 43. Distance between site of landing and the bait. Recorded in Colombia from 1 October 1968 to 15 March 1969.

	Distance between landing site and bait (m)		
Sex and age class	1-3	3-10	>10
Adult male	7	4	2
Adult female	8	6	0
Immature male	4	0	4
Immature female	2	1	1

were less hasty than adults in approaching and departing from the bait. Sometimes condors repeatedly approached and walked away from the bait. Occasionally, they flew without feeding. Once, IM2 landed, stood for 1 minute, flew, landed again 1 minute later, flew 10 to 15 seconds later, and returned once more in 3 minutes. As condors approached the bait, they usually thrust an open beak toward feeding black vultures.

Rates of approach and withdrawal and the sites chosen for take off and landing probably depended on the presence or absence of other individual condors. A number of hasty departures occurred when one condor ran or flew at another (Table 35). In a rare instance of landing right beside the bait, AM1 confronted AM3 in the aggressive exchange described on p. 124. California condors also seem to avoid landing right at or on top of a carcass (Koford, 1953, p. 60).

On mainland beaches in the Paracas area, the approach to food by Andean condors was often prolonged. Occasionally, condors perched on the cliff faces above food items for 1-2 hours before either descending or departing again. Only a few approaches to food varied from the general patterns described above. On three occasions, a condor landed upwind from a dead pelican and walked backwards toward it, a response, no doubt, to the strong 30 to 40 km/hr wind. Feathers would have been ruffled by walking forward with a tailwind. Occasionally, before landing, condors glided back and forth just above the carcass, sometimes moving very slowly at ground speeds of nearly zero. A few approaches were quite abrupt. Early one morning (0618) on Isla Zárate, a group of seven condors on a roosting ledge suddenly dove off together, descended to the beach, and landed at the same place in the midst of a group of sea lions. I could see necks and heads of the condors moving rapidly up and down. A sea lion leaped at them and

chased them away. After five minutes, a sub-adult male condor pulled a dead pup from that site. The sudden and simultaneous descent of the condors from their roost suggests that they may have witnessed a stillbirth.

Manner of Feeding

Tearing of Skin

I saw only adult condors, usually males, tear holes in the skin of bait animals in Colombia. Most of the holes penetrated areas on the forepart of the carcass (Table 44). Of 39 observations of tearing by condors, 34 (87 percent) were by adult males. The male's larger size may explain part of this sex-specific tendency. A female mate may feed in pre-existing openings used prior to her arrival by black or turkey vultures, whereas the male opens new areas. Separation of feeding sites could reduce competition for food between mates and might permit an earlier departure for both birds. Females can use openings torn by the male after he had fed there for a short time. Sites for penetration are likely chosen on the basis of (1) the amount of flesh to be exposed, and (2) the thickness of the skin to be torn. i saw an adult male bite lightly at several places on the shoulder of a horse starting to tear at it. These motions may have served in evaluating these two conditions.

On a number of areas of one dead horse, I measured the thickness of skin to compare the values for tearing sites chosen with other sites on the animal (Figure 29). Although many areas of this animal's skin exceeded 2 mm in thickness, 85 percent of the tearing occurrences listed in Table 44 took place on this horse where the skin was less than 2 mm thick. I also inspected the skin of an adult sea lion (Figure 29b, c). I saw condors tear holes on sea lions only in the axilla

Table 44. Frequency and location of holes torn through the hide of bait animals (horses) by adult condors in the Colombia study area.

Location of penetration	Values for skin thickness (mm)[a]	No. observations	
		Male	Female
Ventral part of lower jaws	1.4	3	3
Lower part of shoulder	1.6-1.9	9	0
Brisket	1.8	5	0
Flank	3.5	4	0
Axilla	1.5	3	1
Ventral part of neck	1.7-2.8	3	0
Side of head			
Jaw	1.3	2	0
Below ear	1.2	1	1
Ventral part of body between front legs	0.9	2	0
Anal area	1.4	2	0
Total		34	5

[a] Recorded on one horse (Fig. 29a).

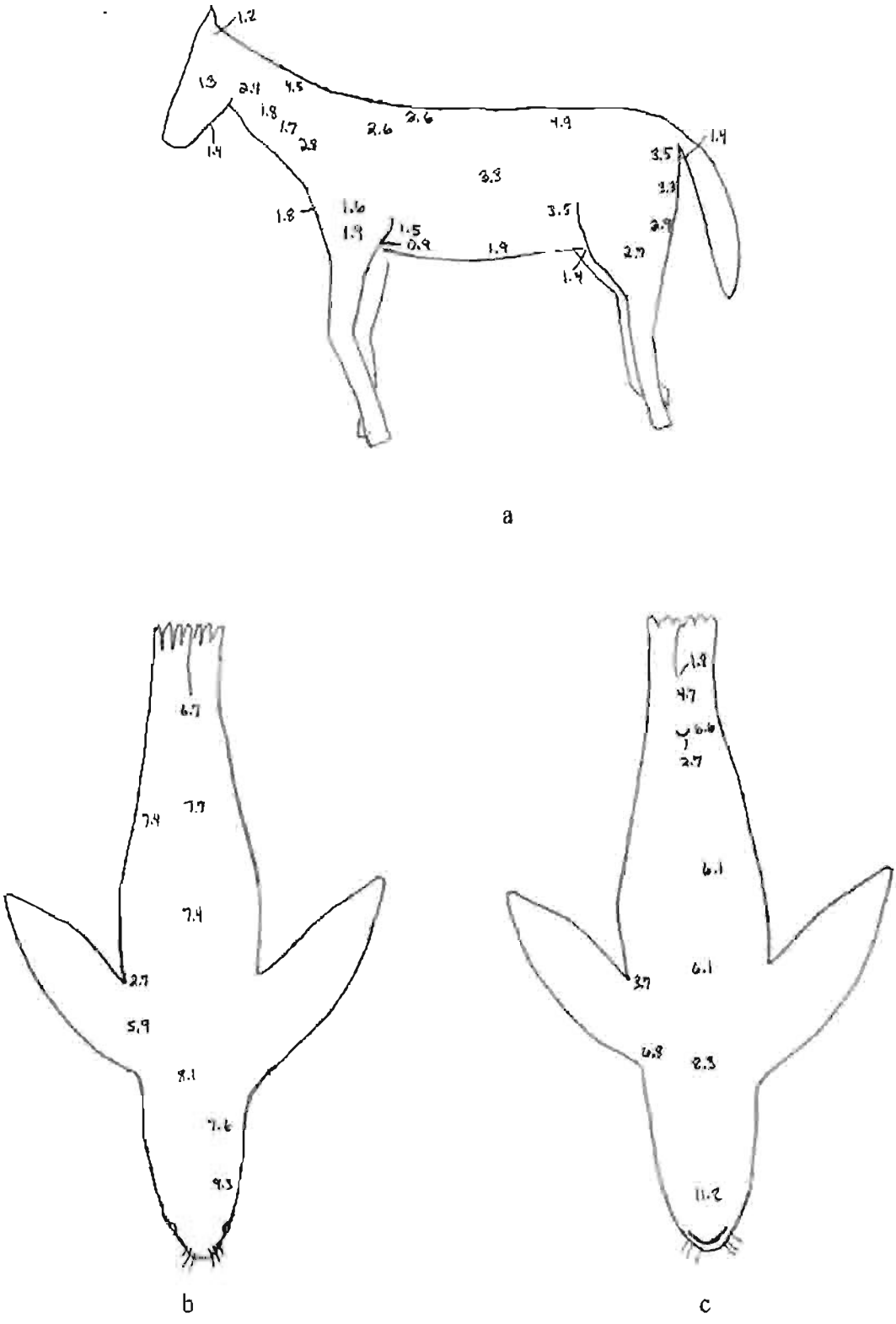


Figure 29. Values for thickness of skin in mm recorded for an adult horse (a) and an adult sea lion about 3 m in length (b, dorsal view; c, ventral view).

area. The thickness of skin measured in the axilla area exceeded only that of the anal region, where an opening already exists. On horses, I saw six instances of ripping on the ventral part of the lower jaws, a region where the skin is relatively thin, but on sea lions, where skin of this area is quite thick, I saw no such attempt.

Two methods of tearing were observed. On the ventral part of the horse's lower jaw, where the skin was relatively thin, the sitting condor usually bit, held the skin in his beak, and then, rocking his body back, ripped a V-shaped opening about 10 to 20 cm in length with one pull. The skin was either grasped near the horse's lip and ripped toward the neck or taken near the posterior part of the jaws and turn forward, toward the horse's mouth. On the higher and thicker side of the shoulder area, the condor stood, either on the ground or on the bait, bit the skin, and pulled until his beak broke loose. Then he grasped it again and pulled in the same way. Most of the holes opened this way required 10 to 15 individual biting motions. When California condors fed on large carcasses, they sometimes tugged as many as 20 times before losing grip (Koford, 1953, p. 61). In my observations of the Andean condors, the bird yanked once before losing hold. The hooked tip of the upper mandible was driven against the stretched skin as the bird lifted his head upward. Apparently, the tip cut the skin as it tore away. Penetration was achieved by pulling at it repeatedly in the same place. Most of the holes opened were oval and about 3 cm by 6 cm. Black vultures usually fed in these openings after the condors had abandoned them. Occasionally, the smaller vultures were able to open areas around the genitalia and anus.

Positions of Legs and Feet

Condors frequently sat on their tarsi while feeding on parts of the carcass near the

ground, like the lower jaw, brisket, flank, or anal area. Feeding in the sitting position is also common with *Gymnogyps* (Koford, 1953, p. 61). The crus of a male Andean condor that fed in the anal part of a horse moved through an angle of about 30^{o} as the bird alternately fed and looked up. When he leaned forward to feed, the crus moved from an angle of about 60^{o} with the horizontal to a vertical position and dropped back again when he looked up. The wrists of his wings extended forward about 10 cm and drooped slightly; wingtips were in a normal position. When condors stood on the ground and pulled at the carcass in a horizontal direction, the feet remained directly beneath the thigh; but the joint between the tarsus and crus of each leg moved inward, laterally, about 5 cm. Standing condors often used one foot to hold down items like sea birds.

Several positions of the legs and feet seemed to be used by feeding condors to increase pulling forces. Condors often stood on the carcass to feed in areas on the upper part of the animal, even though they were easily accessible from the ground. By standing above the feeding hole, they were able to place both legs in line with the direction of pull. Sometimes one foot was placed on the side of the carcass, as the bird, standing on the ground with the other foot, pulled horizontally. A sitting adult female that was feeding on a horse suddenly stood and fell back a step when the flesh she pulled at came free. She remained standing, placed one foot on the side of the carcass, and resumed feeding. The new position probably increased her pulling force and provided better balance by placing some support in line with the direction of action. When condors pulled upward, the neck remained extended, so most of the lifting was done by the legs and back. Sometimes the wings flapped during the pull.

One adult female in the Paracas area fed with difficultly, because she had no left foot and

tarsus. When she pulled at a carcass, her left wing dropped to the ground repeatedly, as she tipped to that side. Sometimes when she pulled upward, the right leg slowly collapsed. Apparently, it was unable to support both her weight and the force of pulling. Another female, an immature bird that limped on one side, used both the strong and weak leg to pull against when she fed.

Movement of Head and Neck

Condors fed with heads upright, turned to the side, or completely inverted. Standing on top of a carcass, they often fed with beaks directed toward their feet and the ventral part of the head facing upward. When a bird stood on the ground and fed in holes that had just been torn open, the head was usually upright. Gradually, however, as the condor moved to one side of the hole, the head turned so that one side of it faced upward and pressed against the inside of the skin. The beak was directed away from the hole toward flesh that had not been taken.

On large animals, condors fed much of the time with their heads and necks inserted through openings in the skin. Usually they cleaned out areas within 40 to 50 cm of each opening, so loose skin then lay on stripped bones. Sometimes a condor struggling to reach pieces far within pushed forward on extended legs and pressed the breast up against the carcass. In this position, the wings were partly extended and the tail elevated above the long axis of the body. Even when feeding on sea birds, condors often inserted their entire head through one small hole. When feathers stuck to the beak of feeding condors, they lifted their heads and shook the feathers off. Occasionally, with some large carcasses, it was unnecessary for either condors or vultures to feed through a small opening. After a few days, the skin sometimes softened where it was in contact with the ground, so both condors and black vultures could tear it easily

along the dorsal part of the ribs. Without penetrating deeply, they fed on the long area of flesh exposed there.

On warm days, the activity of feeding appeared to induce several changes in the condors' appearance. Skin on the head and neck flushed, becoming redder. Nasal secretions often moistened the entire bill, and panting commenced. The head, neck, and collar of those condors feeding deep within carcasses often were covered with blood and bits of flesh (Plate 19). Sometimes the eyes were glazed with a film of blood. Head and neck wiping usually cleaned off most of this material.

Forces Exerted in Feeding

The tugging and pulling action of feeding condors appeared to exert relatively large forces on the carcasses. Sometimes a condor pulled the partly eaten carcass of an adult horse downhill or turned it to one side. One adult lifted and pulled back on the head of a partly eaten horse until it fell and rested on top of the horse's shoulder to expose the side that had been lying on the ground. Using a spring scale to pull carcasses that I had seen condors move, I obtained a few values for the force exerted by feeding condors. An adult male in Colombia exerted a minimum of 165 newtons to move one carcass and an adult female 135 newtons in moving another. Values are minimal because I was unable to record them until the end of the day, after the carcasses had been lightened by continual feeding. In Peru, I saw an adult male drag a dead sea lion pup 45 m down the beach and feed on it for 40 minutes. The weight of the pup after he left was 78 newtons, and the force required to drag it was 59 newtons. Weight consumed after he dragged it was probably at least 7 newtons.

Food Pursuits and Other Activities at Food

When either a condor or black vulture pulled a large piece of flesh free, that bird usually left the carcass and attempted to swallow the piece while running away. Members of both species rushed toward any freshly exposed part, even when a dominant condor carried it. Usually, defense was difficult because of the number of birds in pursuit and the feeding birds preoccupation with swallowing. In one instance, AM1 pulled a long section of flesh from inside the bait and ran to the side with IM2 and 10 to 15 black vultures in pursuit; he swallowed it all before they were able to take any. IF1 once pulled from the horse a strip of tracheal cartilage about 5 cm by 10 cm and ran with it. After a 20-second attempt to swallow it, she dropped it, and the black vultures struggled over it. Pursuits of this type frequently occurred when a bird pulled out a long section of intestine. Additional data on food struggles between condors and black vultures are presented on p. 179.

Body-maintenance activities were common during pauses in the approach and departure and in the intervals between bouts of feeding. Condors frequently preened, sunned, roused, shook, and scratched their heads, gaped, and defecated. Head and neck wiping often followed feeding. Stretching seemed to occur less frequently than in other contexts. I saw one adult female defecate during a feeding bout. An immature male held his wings in the sunning posture for several minutes while he fed. Occasionally, condors courted and copulated at the feeding areas. Several times, I saw immature birds leap about and flap their wings.

Alertness

Condors looked up repeatedly while feeding, probably to assess the possibility of coming danger. It would be difficult for a feeding bird, particularly one with its head buried deep inside

a carcass, to sense changed in the immediate surroundings without frequent and rapid pauses to look about. To obtain a measure of the degree of alertness expressed by feeding birds, I counted the number of times they lifted their heads from the feeding position to a normal stance during 5-minute sampling periods. To obtain another measure comparing the relative weights of feeding and watching, I monitored the total amount of feeding time during each sampling period with a stopwatch that could be stopped and started without resetting to zero. In each sampling period, I recorded data for both measures simultaneously; a summary of the results is presented in Table 45. Then I compared these measures for condors of different sex and age classes and locations and for different avian scavenger species and tested for significant differences; the results of these tests are listed in Table 46.

Sex and Age Class Differences

In Colombia, adult condors looked up more often than immature birds; most rates for the young condors were only about two-thirds those of adults (medians of 22, 23 per 5 minutes compared to 33, 38). Differences were not significant in the amount of time feeding, however, which indicates that adults looked up more often but for shorter durations. Median values for feeding time during 5-min periods ranged from 175 to 208 seconds. Adults were more efficient at being attentive. In the Paracas and Cerro Illescas study areas, adults may have looked up more often than immature females, although differences were not quite significant ($p < 0.10$). Values for feeding time were generally similar, as they were in Colombia,.

I found no significant differences in values of either measure of alertness between adult males and adult females in any of the study areas. Immature males fed for more time during the sampling periods than immature females in Colombia. Most of the data recorded for young

Table 45. Measures of feeding activity and alertness for condors from different study areas and for three other species of avian scavengers. Values recorded for individual 5-min sampling periods when birds fed continuously. No values recorded for birds of those sex and age classes not listed.

		Total feeding time per sampling period			No. times head raised per sampling period		
Birds examined	No. sampling periods	Median	First decile	Ninth decile	Median	First decile	Ninth decile
Condors							
Colombia:							
Adult males	12	191	135	257	33	19	48
Adult females	10	182	130	223	38	17	50
Immature males	19	208	143	242	23	17	34
Immature females	15	175	114	223	22	16	32
Paracas excluding Isla Zarate							
Adult males	5	189	-	-	40	-	-
Adult females	11	197	110	240	33	24	57
Immature females	16	194	136	237	22	9	62
Isla Zárate							
Adult males	14	252	203	281	16	3	43
Adult females	11	245	173	279	26	8	34
Cerro Illescas							
Adult males	3	241	-	-	28	-	-
Adult females	4	192	-	-	42	-	-
Immature females	6	210	-	-	23	-	-
Turkey vultures (Paracas and Cerro Illescas)	23	208	149	274	44	12	75
Black vultures (Cerro Illescas)	15	222	164	274	16	10	24
Peruvian gulls (Paracas)	10	216	152	255	43	27	54

Table 46. Test results for significant differences in the measures of feeding activity and alertness listed in Table 45.. Mann-Whitney tests applied to all comparisons when the median test (using the chi-square and Fisher exact probability tests) failed to reject the null hypothesis.

	Total time fed/sampling period			No times head raised/sampling period		
	U	X^2	p	U	X^2	p
Condor comparisons						
Sex and age class comparison						
Adult male-adult female:						
Colombia	134		>0.1	47		>0.1
Paracas excluding Isla Zarate	15		>0.1	13.5		>0.1
Isla Zárate	73.5		>0.1	55.5		>0.1
Cerro Illescas	4		>0.1	0		0.05<p<0.1
Immature male-immature female						
Colombia	24		<0.002	117.5		>0.1
Adult-immature male						
Colombia	117.5		>0.1			
Adult-immature female						
Colombia	132.5		>0.1			
Paracas	247.5		>0.1	81		0.05<p<0.1
Cerro Illescas	20		>0.1	8.5		0.05<p<0.1
Adult-immature						
Colombia					14.67	<0.001
Location comparisons for adults						
Colombia-Paracas	172.5		>0.1	153		>0.1
Colombia,Paracas-Cerro Illescas	95		>0.1	133		>0.1
Colombia, Paracas, C. Illescas-I. Zárate	123.5		<0.001		14.00	<0.001
Species comparisons						
Turkey vulture-black vulture	136.5		>0.1		24.78	<0.001
Turkey vulture-Peruvian gull				108.5		>0.1
Black vulture-Peruvian gull				Fisher,		<0.001
Turkey and Black v.-Peruvian gull	187		>0.1			
Turkey and black v., Peruvian gulls-adult condors of Colombia, Paracas, and Cerro Illescas		13.16	<0.001			
Turkey and black v., Peruvian gulls-adult condors of I. Zárate		8.56	<0.01			
Turkey v. and Peruvian gulls-adult condors of Colombia, Paracas, and Cerro Illescas					4.33	<0.05
Black v.-adult condors of I. Zárate				138		over 0.1

males in Colombia, however, involved IM2 and IM3; feeding together as they often did may have acted in suppressing some attentiveness.

Location Comparisons

Difference in values describing adult alertness in the Colombia, Cerro Illescas, and Paracas study areas were not significant, if birds observed on Isla Zárate were excluded from the comparison. For both measures of alertness, the differences between values recorded on Isla Zárate and those of other areas were highly significant. On this tiny island, a refuge only about 200 m in length, condors were safe from any human intrusion. Here, the same population monitored on the mainland coast behaved in a more relaxed manner. They lifted their heads about half as often as the birds on the mainland across the channel. For most, feeding time comprised more than 80 percent of the sampling period, whereas condors on the mainland usually fed for only about two-thirds of that time period (189 to 197 seconds compared to 245 to 252 sec). The alertness displayed by feeding condors seems, then, to be more for protection from humans than a social response to the presence of other condors. In northern Rhodesia, Attwell (1963) noted a marked difference in the timidity of five species of Old World vultures in two different locations but was unable to offer any reason for its occurrence.

Comparisons With Other Avian Scavengers

I found no significant differences in values for feeding time among turkey and black vultures and Peruvian gulls. As a group, however, these species fed for a significantly shorter time than the Isla Zárate condors and significantly longer than the adult condors of the other areas. I made no location comparisons for these species, however, so the expression of alertness may be as flexible as that of the condor. Black vultures lifted their heads at a significantly lower

rate than either of the two smaller scavenger species; thus, most bouts of watching by black vultures were more prolonged. The highest rates of head lifting recorded among all the scavenger species were for turkey vultures and Peruvian gulls; I obtained median values of 44 and 43 times per 5-min sampling period, respectively. One turkey vulture looked up 82 times during the sampling period; a mean interval of less than 4 seconds interspersed these instances of watching. Most of the rates for turkey and black vultures were recorded at the same baits during the same periods, so the low rate of head lifting by the black vulture relative to the turkey vulture seems a fair measure for this difference in 'temperaments,' even though rates for both species might be as variable as those of the condor.

Other Possible Variables

Using data on both condors and turkey vultures, I searched for but found no significant relationship between the rates of head lifting and the presence or absence of other conspecific individuals. Birds of a large group are likely to detect and avoid danger sooner than a lone individual; this possible suppressing effect by group influence on the rate of head lifting may be countered slightly, however, by a presence and pressure of social exchange. Subordinate birds in large groups may be particularly attentive. Unfortunately, sample sizes in this study were too small to examine for the effects of these related conditions. As noted before, however, data from Isla Zárate suggest that head lifting is less a social response than it is a protective one against human intrusion.

Although we gathered no other quantitative data on this question, I noted a few other factors that seemed to influence the rates of watching and feeding. Birds feeding on the higher parts of the bait appeared to look up more frequently but for shorter durations than those feeding

near the ground. Intense activity by black vulturesmay also have caused condors to look up more often. Rates of head lifting appeared to decline when fleshy parts of a carcass became more accessible. As crops began to fill, feeding birds seemed to move more slowly, look up less often and for longer durations.

Duration of Feeding Bouts and Visits

In Colombia, we kept records on the frequency and duration of bait visits and feeding bouts by individual condors, a summary presented earlier in Table 25. For both immature males and females, the number of feeding bouts exceeded the number of bait visits (males, 155 visits and 200 bouts; females 21 and 36), whereas the reverse was true for adults of both sexes (males, 167 visits, 132 bouts; females 145 and 136). Immature birds often fed, moved off the bait when adults or other dominant individuals arrived, and returned when they left. Adults usually fed only once after arriving; sometimes they left without feeding at all. The mean visitation duration for adult males was only 6.4 minutes, compared to 25.8 minutes for immature females. Visits by members of this dominant class were significantly shorter than those of any other sex and age class.[2] With priority of access to food assured, the dominant adult male could land, feed, and depart without hesitation. Durations for both the visit and the feeding bout by adults were significantly shorter than those of the younger, subordinate birds.[3] The longest visit at the Colombian baits was 109 minutes by IM3, and the longest feeding bout was 66 minutes by IF1. Koford (1953, p. 61) once saw a California condor feed on a cow for 1 hour.

The variability in visitation durations at the Colombian baits was about the same for male and female and for adult and immature birds, whereas durations for the period of feeding

appeared to be more consistent for adults of both sexes than for immature birds. The coefficient of variability for feeding durations was highest for immature females (137) and lowest for adult females (88).

Other Feeding Characteristics

Feeding Area on the Carcass

In Colombia, I recorded how often different areas of the bait were fed on by individual condors (Table 47). More than half of the occurrences recorded (58 percent) involved feeding areas anterior to and including the shoulders and axillae. More flesh may have been available in the forepart of the bait animals, most of which were horses. Black vultures were able to feed extensively in the groin and anal parts of most baits without recourse to holes torn open by condors. Because feeding by these smaller vultures occurred almost continuously during all hours of daylight, it is likely that more flesh had been taken in the posterior part of the bait before condors arrived. I searched for but found no significant tendencies by any of the individual condors listed in Table 47 to feed in certain areas more often than others. I did find, however, that the distribution of feeding occurrences by adult males, adult females, and immature birds, considered as three groups, did vary from that expected according to locale on the bait.[4] In the major departures of this test, adult females, relative to the others, apparently preferred to feed more often on the head and neck and less often in the area of the shoulder, brisket, and axilla, whereas adult males preferred this latter area. The shoulder region was a favorite place for tearing the skin, and adult males accounted for most of the skin-tearing occurrences observed (87 percent, Table 44).

Table 47. Frequency of feeding occurrences on different parts of the baits in the Colombia study area.

Bait area fed on	Percent feeding occurrences observed for: IM2	IM3	Other immature males	Immature females	AM1	AM3	Other adult males	Adult females	Total no. observations
Head and neck	33	49	36	25	42	47	26	51	137
Brisket, shoulder, axilla	17	21	17	8	23	24	26	9	62
Back, belly, flank, groin	13	11	12	33	8	18	25	14	54
Anal area	37	19	36	33	27	12	23	26	93
Total no. observations	52	47	42	12	26	17	65	85	346

Departing

In departing, condors that did not appear alarmed, usually walked uphill before they took off; they moved up the side of the gulley over the Colombian baits or climbed the sandy slopes and rocky outcroppings on the Peruvian coast. The additional altitude on slopes eased take off, particularly for condors with full crops. One adult female in Colombia climbed the hill above the bait and then, flapping her wings, ran downhill for 15 m before finally becoming completely airborne.

Three condors that I surprised feeding on one Peruvian beach climbed 60 m up a sandy slope before flying. An undisturbed condor climbed 20 m up this slope after feeding and before taking off; he wiped his head and neck in the sand for 10 minutes during one interval of the climb. Alarmed birds flew from where they fed. In Colombia, these sudden departures occurred whenever black-chested buzzard-eagles glided overhead and black vultures rushed to congregate in a mass over the carcass. Condors also took off suddenly when another flying condor dove down upon them.

Regurgitation

Pellets containing indigestible items like feathers were sometimes regurgitated by condors. Condors cast these pellets less frequently than most birds of prey, probably because they fed through holes in the carcass and picked up fewer feathers or less hair on the flesh they swallowed. Many birds of prey tear the skin or pluck feathers from the animals they consume and inadvertently swallow a large proportion of indigestible material. Only once did I see a wild condor cast a full pellet. The pellet, dropped in a cave in the Cerro Illescas area, was 7.5 cm in length and 3.0 cm in diameter and contained feathers of a pelican and skin from the feet. In

another cave of the Cerro Illescas, where condor tracks marked the sand and condor feathers lay about, I found a pellet 10 cm in length and 3 cm in diameter containing pelican breast, neck, and wing covert feathers and, again, skin from the feet. None of the feathers exceeded 5 cm in length. Five other pellets taken from one other cave in this study area may have been cast by either turkey vultures or condors. They varied from 2 to 3 cm in diameter and from 4 to 6 cm in length and contained feathers from a pelican and some other unidentified bird(s), a circular piece of bone 2.5 cm in diameter (from the skull of a bird?), wood chips, and a few strands of hair. Irregularly, the captive immature male condor regurgitated pellets of plant material, usually grass stems and leaves. Rea (1973) found pellets cast by turkey vultures often contained the remains of small mammals and birds.

Predatory Behavior

Although I never witnessed it, wild Andean condors apparently kill prey on rare occasions. Both turkey and black vultures have been reported to attack live prey (McIlhenny, 1939; Hamilton, 1941; Sprunt, 1946; Lovell, 1947; Mueller and Berger, 1967; Glading and Glading, 1970), but there are no records for California condors doing so (Koford, 1953, p. 55). Local people in the Colombia study area claimed that Andean condors sometimes liked newborn calves, and a goathered in the Cerro Illescas said that he lost newborn goats to condors annually. Koford (1957) doubted that Andean condors would kill the healthy newborn of large mammals, until he saw 14 condors land beside a vicuña giving birth. Several other pregnant vicuñas rushed at approaching condors. Not until the juvenile vicuña was standing a half an hour after bird did the condors depart.

In Ecuador, Wiggins (1945) saw three condors drop into a distant draw where a dead calf

was found later. He examined the dead animal judged that condors had killed it. In Colombia, I saw an adult pair land within 7 m of a sleeping calf after circling over it for several minutes. When the second condor landed, the calf rose and ran to a group of cows about 40 m distant. Both condors flew then. On a number of occasions, we saw condors on Isla Zárate bite and sometimes pursue young sea lions.

Occasionally, condors prey on other birds. Murphy (1925, p. 189-190) reported condor depredations on Peruvian diving petrels. Apparently the condors stood near the petrel burrows and caught them as they came out. He also witnessed the effects of egg destruction on colonies of the guanay cormorant by avian scavengers, of which the condor was an important contributor.

"When I landed upon Asia Island, off central Peru, on December 4, 1919, great destruction of guanay eggs had been wrought by gulls, turkey vultures, and condors. Although a colony containing countless eggs and young still covered about half of the western slope, extending from the summit almost to the water, and filling a deep ravine as well as the rounded hillside, the other half had become a waste of empty nests and broken egg-shells, and had been deserted for the season by the parent birds . . . In the heart of the colony stood a condor with a small circle of abandoned and rifled nests round about. When this pilferer had been shot and picked up by the feet, the albumen and mostly unbroken yolks of a round dozen of fresh eggs slide out of its gullet. Scarcely any pieces of shell were visible in this rich meal, the supposition being that the condors must such the contents of the eggs through their trough-shaped tongues." (pp 88-89)

Guano island wardens have reported that when condors glide overhead, the nesting sea birds flee from their nests, break eggs, and kill young. I saw several thousand perched Inca terns take off when a condor landed near them. On another occasion, 150 pelicans took off in haste when a condor landed 5 m from them. Individual groups of Peruvian boobies perched along a long column of cliffs took off one at a time when an adult condor glided by, passing 5 to 10 m from their perches. In the Barranco zoo of Lima, I saw an adult male condor pull a sick hawk under the netting from a neighboring cage, carry the nearly dead bird around the cage, and nibble

at the hawk's breast and wing. The condor moved cautiously, holding his writs 2 to 5 cm out from the body and standing and walking in a very erect stance. My captive immature male condor caught a crippled domestic duck and tore skin from the back and neck of the duck before he was able to escape. In one zoo, a live rabbit released in a cage with two adult condors was pursued, caught, and fed upon immediately (Gailey and Bolwig, 1973).

Effects of Disturbance

Feeding condors were often easily disturbed. Normally, they neither fed nor alighted if humans were near and visible. On a number of occasions in all three study areas, condors fled from our baits when humans appeared, either on foot or in cars. Several times in the Paracas area, however, we did see condors feed when humans were visible within 1 km. A group of condors continued to feed on one beach near Laguna Grande after I drove to within 1 km and stopped; another vehicle also passed them at the same distance. I once saw an adult female land on the beach within 300 m of the village of Lagunillas; the village was active with cars, boats, and people in motion. She flew without feeding.

The response of feeding condors to some surrounding activities varied markedly. Condors flew from the Colombian baits on six of eight occasions when low-flying airplanes passed overhead; yet in one instance, the condors only looked up for a moment and then resumed feeding, and in another, an adult female did not even look up but continued to feed without any pause. Fishing launches passing near Isla Zárate also evoked divergent responses by the condors feeding there. Three condors flew from the island and landed on another rocky prominence just south of the island once when two boats passed by. In three other separate incidents, condors ran or flew up to a 15 m when a boat moved through the Zárate Channel. In another instance,

however, a group of feeding condors made no apparent response at all to five launches that traveled by a single file.

Frequently, the sounds of other birds disturbed feeding condors. Three condors ran from one carcass and crouched with wings partly extended after one adult shook his body. In another case, a condor ran from a bait following the body shake of a nearby turkey vulture. Condors often ran or flew when black vultures moved rapidly, a frequent occurrence whenever new feeding areas on the carcass were opened. Sometimes vultures that were landing or taking off appeared to startle condors. I saw a condor jump and wheel around when a gull cried out. Rocks feel when a turkey vulture landed on a nearby cliff in the Cerro Illescase, and an adult male at the bait flew immediately. In Colombia, black vultures rushed into a tight group over and around the carcass whenever a black-chested buzzard-eagle soared overhead. On 18 separate occasions, condors were frightened from the bait by this sudden burst of gathering activity.

Other animals often disturbed. Dogs, horses, or cattle occasionally interrupted feeding condors in Colombia. Sometimes, on Isla Zárate, condors retreated from carcasses where they fed when sea lions pursued them. The surf rarely alarmed condors on the coast, although occasionally they did respond to large breakers. On Isla Zárate, water from one breaker splashed up on a carcass where three condors fed. Flapping their wings, they ran up a rocky bank behind. After a moment, they returned to feed again. A feeding condor flew 15 m when a large breaker fell near him.

AVIAN SCAVENGERS ON THE PARACAS COAST

Food Supply

The Food Survey

The study area comprised one tiny island, Isla Zárate, and 98.8 km of coastline that ran a straight-line or map distance of 45 km (Figure 4). A series of l2 cliff chains, ranging from 3 to 300 m in height and 1.5 to 16.7 km in extent, stands along 76.6 km or 78 percent of this section of coast. The cliffs are separated by 12 open beaches that range from 0.7 to 5.6 km in extent. Food available and consumed on these open beaches was estimated by sampling three beaches daily, one week each month for seven months. Beaches or parts of beaches were considered as one of three types: (1) Two human-inhabited segments of beach together were 2.5 km in length. These segments, representing the two fishing villages of Lagunillas and Laguna Grande, were not considered in the study. (2) Two bay-protected beaches, representing 5.8 km of coastline, acted as refuges for sick and dying birds. One of these beaches, 4.3 km long, was sampled (Beach A). (3) Of the beaches and beach segments that remained, two were selected randomly for sampling. Beach B is 2.4 km long and C, 1.3 km. For 19.7 km of beach stratum considered in the study, 8 km or 41 percent were sampled.

Food Mass Available

I obtained estimates for the biomass of each bird species available to scavengers on the sample beaches by multiplying the number of specimens found by a value for the edible mass of that species (Table 48). Figures for mass of inedible parts presented in Table 48 were secured by weighing the undried skin, skeleton, and feathers for specimens of each species listed. The brain, bone marrow, tendons, and ligaments, and tiny pieces of flesh in the neck and a few other places all contributed to the mass considered unavailable to the scavengers of that area. Although I used only mean values to compute edible mass, the standard error of the mean (s_x or

Table 48. Edible mass of bird species commonly found on the sample beaches. Paracas, Peru 1969-70.

	Total fresh mass (g)		Mass of inedible parts (g)[a]		Edible mass (g)
	n	Mean ± S.E.	n	Mean ± S.E.	
Guanay cormorant	24	1,400 ± 34	3	600 ± 35	800
Peruvian booby	16	870 ± 29	1	500	370
Brown pelican	9	4,100 ± 280	1	2,300	1,800
Humboldt penguin	5	5,900 ± 220	2	2,000 ± 125	3,900

[a] Undried skeleton, skin, and feathers.

S.E) is provided here and in a few other instances in this ecology study to provide an idea of the variation in the sample. Humboldt penguins provided more edible mass than the others, 3900 g on the average, followed by the brown pelican with 1800 g and the guanay cormorant with 800 g. I weighed most mammal, reptile, and fish specimens individually and estimated the biomass available directly. In the case of large sea lions, I had to estimate biomass available without any spring balance recordings. Values for the food mass available during seven census weeks on sample beach A are presented in Table 49; those of sample beaches B and C are in Table 50.

Sea lion comprised the greatest part of the food available during the entire study period, representing 1094.5 kg on the three study beaches, about 76 percent of the mass of all food tallied, although fresh sea lion, preferred by avian scavengers, represented only 219.5 kg or 15 percent. Guanay cormorants were second, representing 86.4 kg or 6 percent, and all birds combined comprised 12 percent of the food available (169.1 kg). Most of the birds were available during August and September, whereas sea lions were more dispersed throughout the period of study.

Food Mass Consumed

During the food census, I weighed and marked each specimen found on the sample beaches. On the census days following, I weighed marked specimens repeatedly until all of the edible parts had been consumed or the specimen had been washed back into the sea or covered with sand. Total differences in day-to-day weights or marked specimens were taken to represent the mass consumed by avian scavenger species. Biomass taken from the few partially skinned specimens that had been fed on by an occasional fox was not considered in this survey. Data on the amount of food mass consumed during the weekly sampling periods for beaches A, B, and C

Table 49. Food mass in g available during seven 1-week periods on sample beach A, Paracas, Peru 1969-70. Sampled during second or third week of each month.

	Birds												Mammals				Reptiles	
	Guanay cormorant		Peruvian booby		Brown pelican		Humboldt penguin		Other birds		Total birds		Sea lion (fresh)		Sea lion (decomposed)		Green turtle (decomposed)	
	n	Total mass(g)[a]	n	Total mass(g)[a]	n	Total mass(g)[b]	n	Total mass(g)[b]	n	Total mass(g)[c]	n	Total mass(g)[a]	n	Total mass(g)[a]	n	Total mass(g)[b]	n	Total mass(g)[c]
August	65	52,000	65	24,050	13	23,400	0	0	2	1,380	145	100,830	0	0	1	65,000[c]	0	0
September	38	30,400	2	740	6	10,800	0	0	2	1,010	48	42,950	0	0	1	450,000[c]	0	0
October	0	0	0	0	0	0	0	0	0	0	0	0	1	9,100	1	450,000[c]	0	0
November	1	800	0	0	0	0	0	0	0	0	1	800	0	0	0	0	0	0
December	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
January	0	0	0	0	0	0	5	19,500	2	200	7	19,700	0	0	0	0	0	0
February	3	2,400	0	0	0	0	0	0	0	0	3	2,400	0	0	0	0	1	5,000
Total	107	85,600	67	24,790	19	34,200	5	19,500	6	2,590	204	166,680	1	9,100	3	515,000[d]	1	5,000

[a] See Table 48.

[b] Two Peruvian diving petrels, one red-legged cormorant, one giant fulmar, one southern fulmar, and one gray gull.

[c] Estimated mass—no actual recording with a balance.

[d] One animal recorded twice is represented in the total once only.

Table 50. Food mass in g available during seven 1-week periods on sample beaches B and C, Paracas, Peru 1969-70. Sampled during second or third week of each month.

	BEACH C												
	Mammals				Birds								
	Sea lion (fresh)		Sea lion (decomposed)		Fish[a] (fresh)		Guanay cormorant		Humboldt penguin		Sea lion (fresh)		Fish[b] (fresh)	
Month of Sample	*n*	Total mass(*g*)[c]	*n*	Total mass(*g*)	*n*	Total mass(*g*)	*n*	Total mass(*g*)	*n*	Total mass(*g*)	*n*	Total mass(*g*)	*n*	Total mass(*g*)
August	0	0	0	0	0	0	0	0	0	0	0	0	0	0
September	0	0	0	0	0	0	0	0	0	0	0	0	0	0
October	1	60,000[d]	0	0	0	0	0	0	0	0	1	10,000	0	0
November	0	0	1	60,000[d]	1	380	1	800	0	0	1	10,300	0	0
December	0	0	0	0	2	760	0	0	0	0	0	0	0	0
January	0	0	1	300,000[d]	0	0	0	0	0	0	0	0	22	5,340
February	1	130,000[d]	0	0	1	700	0	0	1	1,600[e]	0	0	3	4,900
Total	2	190,000	2	360,000	4	1,840	1	800	1	1,600	2	20,300	25	10,240

[a] Two grunt, one ray (*Dasyatidae*), one eel (*Muraenidae*).
[b] Five rays (*Dasyatidae*)
[c] See Table 48.
[d] Estimated mass—no actual recording with a balance.
[e] Partially eaten before it washed onto the sample beach.

are presented in Tables 51 and 52. Estimates for the total food mass consumed per week on all beaches of the study area were obtained by extrapolating with a proportion relating the length of the sample beaches to all beaches in the study area (Table 53). Total estimated mass of guanay cormorants consumed was about 43 kg, approximately 24 percent of the total biomass consumed. All birds combined represented 94 kg or 52 percent, and sea lions comprised 19 percent of the biomass, of which only four percent came from sea lions that were in advanced states of decomposition.

To obtain a measure of food preference by avian scavengers I computed the percent consumed of each food species available, ranking those with the higher percentages as the species most preferred (Table 54). The preference ranking obtained should be considered with some caution, however, for the monthly variations in the species available, together with fluctuations in the amount of food available, might have biased the comparisons. For example, dead Humboldt penguins were found only in the months of January and February when dead birds of other species were rare; a high percentage of penguin mass consumed might be related to a reduction in the total food mass available per scavenger during these two months, compared to earlier months of the study when other birds were available. Conversely, a low proportion for the mass consumed of a preferred species might be due to an abundance of food during the period when that species was available.

Scavenger Feeding

Diet Composition

On the Paracas study area, the diet of condors was composed mostly of mammals (79

Table 51a Food mass in g consumed by avian scavengers during seven 1-week periods on sample beach A, Paracas, Peru 1969-70. Sampled during second or third week of each month.

	Avian Food Mass Consumed																	
	Guanay Cormorant			Peruvian booby			Brown pelican			Humboldt penguin			Other birds[a]			Total birds		
Month of Sample	n[b]	Mean ± S.E.[c]	Total mass consumed	n[b]	Mean ± S.E.[c]	Total mass consumed	n[b]	Mean ± S.E.[c]	Total mass consumed	n[b]	Mean ± S.E.[c]	Total mass consumed	n[b]	Mean ± S.E.[c]	Total mass consumed	n[b]		Total mass consumed
August	55	368±29	20,210	32	127±14	4,060	18	68±128	12,250	0	0	0	1	210	210	106		36,730
September	26	294±43	7,640	1	400	400	7	429±127	3,000	0	0	0	3	363±218	1,090	37		12,130
October	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0
November	1	640	640	0	0	0	0	0	0	0	0	0	0	0	0	1		640
December	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0
January	0	0	0	0	0	0	0	0	0	6	2408±712	14,450	2	100±0	200	8		14,650
February	2	700±100	1,400	0	0	0	0	0	0	0	0	0	0	0	0	2		1,400
Total	84		29,890	33		4,460	25		15,250	6		14,450			1,500	154		65,550

[a] Two red-legged cormorants, one southern fulmar, two diving petrels, one gray gull.

[b] Minimum number of total feeding instances by avian scavengers on individuals of the species designated.

[c] Mean and standard error for mass of one individual consumed in one day.

Table **51b.** A continuation from 228a.

Mammals						Reptiles		
Sea lion (fresh)			Sea lion (decomposed)			Green turtle (decomp.)		
n^b	Mean ± S.E.[c]	Total mass consumed	n^b	Mean ± S.E.[c]	Total mass consumed	n^b	Mean ± S.E.[c]	Total mass consumed
0	0	0	1	200	200	0	0	0
0	0	0	5	180±106	900	0	0	0
4	1850±501	7,400	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	3	500±153	1,500
4		7,400	6		1,100	3		1,500

Table 52a Food mass in g consumed by avian scavengers during seven 1-week periods on sample beaches B and C, Paracas, Peru 1969-70. Sampled during second or third week of each month.

	BEACH B												BEACH C		
	Mammals						Fish[a]			Birds					
	Sea lion (fresh)			Sea lion (decomposed)			Fish (fresh)			Guanay cormorant			Humboldt penguin		
Month of Sample	n[c]	Mean ± S.E.[d]	Total mass consumed	n	Mean ± S.E.	Total mass consumed	n	Mean ± S.E.	Total mass consumed	n	Mean ± S.E.	Total mass consumed	n	Mean ± S.E.	Total mass consumed
August	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
September	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
October	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
November	0	0	0	1	400	400	1	0	80	1	800	800	0	0	0
December	0	0	0	0	0	0	1	0	600	0	0	0	0	0	0
January	0	0	0	2	500±100	1,000	0	0	0	0	0	0	0	0	0
February	2	400±200	800	0	0	0	2	115±85	230	0	0	0	3	267±33	800
Total	2		800	3		1,400	4		910	1		800	3		800

[a] Two grunt, one ray (*Dasyatidae*), one eel (*Muraenidae*).

[b] Mullet, two rays (*Dasyatidae*)

[c] Minimum number of total feeding instances by avian scavengers on individuals of the species designated.

[d] Mean and standard error for mass of one individual consumed in one day.

Table 52b. A continuation from 228c

Mammals			Fish		
Sea lion (fresh)			Fish[b] (fresh)		
n	Mean ± S.E.	Total mass consumed	*n*	Mean ± S.E.	Total mass consumed
0	0	0	0	0	0
0	0	0	0	0	0
3	933±133	2,800	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	1	50	50
0	0	0	2	500±300	1,000
3		2,800	3		1,050

Table 53. Estimates of the biomass (*g*) consumed per week by avian scavengers along 22.2 km. of Peruvian beach. (Values from Table 51) x (5.8km./4.3km.) + (Values from Table 52) X (13.9km/3.7km.).

	August	September	October	November	December	January	February	Total
Guanay cormorant	27,260	10,310	0	3,870	0	0	1,890	43,330
Peruvian booby	5,480	540	0	0	0	0	0	6,020
Brown pelican	16,520	4,050	0	0	0	0	0	20,570
Humboldt penguin	0	0	0	0	0	19,490	3,000	22,490
Other birds	280	1,470	0	0	0	270	0	2,020
Total birds	49,540	16,370	0	3,870	0	19,760	4,890	94,430
Sea lion (fresh)	0	0	25,000	0	0	0	3,000	28,000
Sea lion (decomp.)	270	1,210	0	1,500	0	3,760	0	6,740
Green turtle (decomp.)	0	0	0	0	0	0	2,020	2,020
Fish (fresh)	0	0	0	300	2,250	190	4,620	7,360
Total	49,810	17,580	25,000	5,670	2,250	23,710	14,530	181,880

Table 54. A measure of food preference by avian scavengers calculated from the ratio of that eaten to that available.

Food Species	Total amount of edible biomass recorded on the three sample beaches. (Tables 49,50)	Total amount of biomass consumed on the three sample beaches. (Tables 51, 52)	Percent consumed of that available	Preference ranking
Guanay cormorant	86,400	30,690	35.5	4
Peruvian booby	24,790	4,460	18.0	6
Brown pelican	34,200	15,250	45.0	3
Humboldt penguin	21,100	15,250	72.3	1
Other birds	2,590	1,500	58.0	2
Total birds	169,080	67,150	39.7	
Sea lion (fresh)	219,500	11,000	5.0	8
Sea lion (decomposed)	875,000	2,500	0.3	9
Green turtle (decomposed)	5,000	1,500	30.0	5
Fish (fresh)	12,080	1,960	16.2	7

percent), usually sea lions (50 percent, Table 55, Figure 30). Mammals figured in the majority of feeding observations for turkey vultures as well (56 percent). Birds, however, were fed upon comparatively more often by these smaller vultures (32 percent) than by condors (21 percent). I saw condors feeding only on birds and mammals in this area, whereas turkey vultures were also seen to feed on turtles, fish, and human refuse. Differences in the data recorded on diet composition for condors and turkey vultures were significant.[5] Two-thirds or more of the feeding observations for gulls involved fish or invertebrate organisms as food. Human refuse composed about a quarter of the gull diet in that area, whereas birds and mammals represented a much smaller fraction, less than 10 percent, of the diet. I found no significant difference between diets of the two gull species, as represented by the sightings we made along the beaches.[6]

Rates of Ingestion

I calculated mean rates of ingestion with data on the duration of feeding period and on the weight of a food item before and after the feeding bout by a wild scavenger. Adult male-female condor pairs fed on a sea lion at a mean rate of 5 g per minute per condor and Humboldt penguins at rates of 51 and 49 g per minute, whereas an immature female fed on a penguin at a rate of 38 g per minute. Turkey vultures ingested sea lions at a rate of 12 g per minute and guanay cormorants at rates of 6, 8, and 20 g per minute, whereas Peruvian gull rates on a guanay cormorant were 1 and 6 g per minute. On the average, for a given unit of time, condors ingested approximately five times the amount taken by turkey vultures (47 g per minute; 10 g per minute); whereas the rate for the smaller vulture was about twice that of the Peruvian gull (4 g per minute).

Table 55. Diet composition of four avian scavenger species. Percent of feeding occurrences observed listed according to the type of food. Recorded along 22.2 km. of Peruvian beach from August 1969 to February 1970.

	Birds				Mammals		Other					Total No. feeding occurrences observed
	Guanay cormorant	Peruvian booby	Brown pelican	Humboldt penguin	Sea lion	Burmeister's porpoise	Green turtle	Fish	Invertebrates	Unknown	Human refuse	
Condor	6	4	9	1	59	21	0	0	0	0	0	68
Turkey vulture	12	1	4	15	52	4	6	4	0	0	2	140
Peruvian gull	1	0	1	2	2	0	0	13	54	1	27	162
Kelp gull	2	0	0	2	0	0	0	26	28	17	26	58

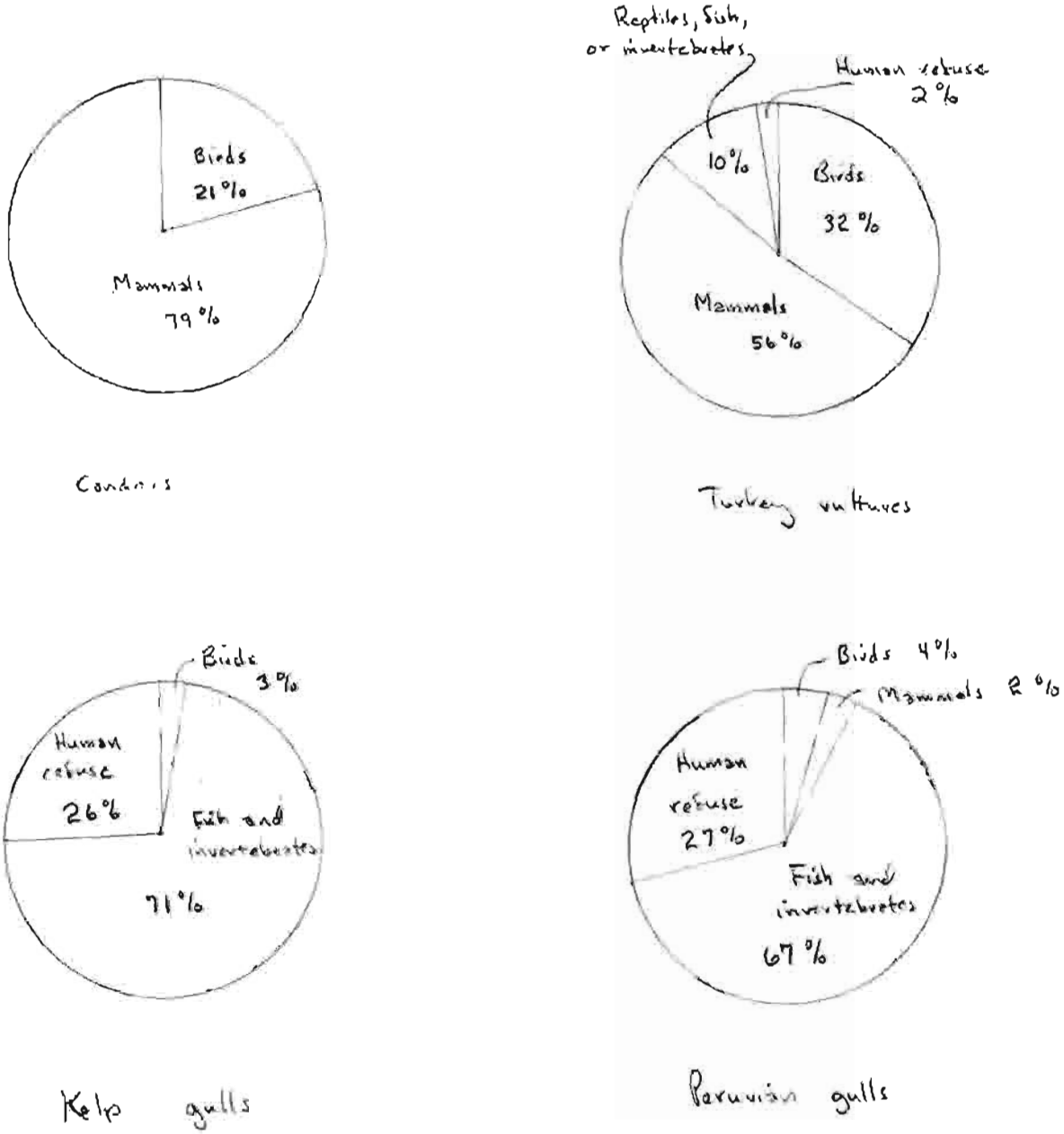


Figure 30. Diet composition computed from feeding observations on four scavenger species in the Paracas study area. Figures are approximations. Data from Table 55.

The rate of ingestion for each species must depend, to some extent, on the accessibility of flesh on the carcass. The importance of different factors determining accessibility probably varies for each scavenger species. These factors likely include the type and size of the prey item, the amount of flesh remaining and its stage of decomposition, the relative amount and position of obstructive material like bone or skin, and external factors like the number of other feeding birds and the location of the carcass. Condors feeding on Isla Zárate illustrate how the last factor might operate; these birds were likely to ingest at greater rates than those on the mainland because they looked up less often (p. 216).

Other differences in the rates of ingestion among conspecific birds are probable, even in comparable situations. In observations from the blind, adults seemed to move more rapidly when feeding than the younger birds. The three rates of about 50 g/min recorded for adults are quite similar in magnitude any may represent a maximum level for the ingestion on muscle tissue of carcasses on the mainland. In comparison, a smaller value of 38 g/min recorded for an immature female may be more characteristic of younger, less experienced birds. The duration of feeding bouts by adult condors in the Colombia study area tended to be shorter than those of immature birds (Table 25); rates of ingestion by adults must have been greater if amounts consumed were comparable.

Rates of Crop Emptying

I obtained estimates on the rate of crop emptying for condors by observing a captive immature male in the Paracas study area. I measured the size of the condor's crop over intervals ranging from 1 to 23 hours and recorded values for the change in volume per hour. For 11 sampling periods, the mean interval between measurements was 2 hr. Rates of change in the

volume of the crop ranged from 5 to 100 cm3/hr, with a median of 40 cm3/hr and a mean and computed standard error of 42 + 9 cm^3/hr. Using a density value for muscle of 1.1g/cm^3, provided by the Meat Science Department of the University of Wisconsin, I translated units of volume to units of mass to secure a mean estimate for the rate of emptying as 46 g/hr with 95 percent confidence limits of 24 and 68 g/hr. Houston and Cooper (1975) obtained a similar estimate of 1200 g emptied in 28 hours by a white-backed vulture, a rate of about 43 g/hr.

Food Mass Consumed Daily

I recorded values for the food mass consumed by members of the four scavenger species held captive within the study area during the food-ecology study (Table 56). Data were taken and are presented on a daily basis. An immature male condor consumed an average 480 g per day compared to 330 g for a turkey vulture and 130 g for each of four gulls (two Peruvian and two kelp gulls). The amount of food mass consumed often appeared to be inversely related to amount taken on the day preceding and the day following. For example, when the mass consumed by an individual exceeding the daily average, then the amount taken on the following day was often less than average. Hence, variation about the mean for the food mass consumed daily is probably markedly higher than what would have been obtained for longer sampling periods. Confidence limits given in Table 56 are probably higher than comparable levels for weekly measures of food mass consumed, a unit employed in the latter part of this study.

Values for the maintenance diet of turkey vultures in Virginia obtained by Prater *et al*. (1976) approximated 140 g, less than half of that recorded in Peru. Climatic or racial differences may explain part of the difference. However, my data were recorded with only a single subject sampled over a 6-day period. When this value is used later to gain other estimates of feeding

Table 56. Food mass consumed daily by captive avian scavengers. Data recorded in the Paracas study area from August 1969 to February 1970.

Subjects observed	Mean mass of the scavenger (*g*)	No. sampling days	Mean and standard error for food mass consumed daily	Confidence limits (0.95) for the mean food mass consumed daily
One immature male condor	9,400	28	480±70	340,630
One turkey vulture	1,885	6	330±40	220,440
Two Peruvian and two kelp gulls	700	8	130±20	90,180

dynamics, I include, for comparison, results secured using figures from Prather et al.

Scavenger Populations and Food

Scavenger Population Sizes

Six times during the study, a monthly census of scavenger populations was conducted along the coast of the entire study area (Table 57). Condors, turkey vultures, and many gulls roosted on cliffs facing the sea; by traveling in a boat beneath the cliffs during the morning hours of 0530 to 1030, two of us were able to count the number of birds present there. Simultaneously, in separate boats, each of us censused coastline along half of the study area. All cliffs in the study area were visible from sea routes taken on the census, so the number of condors counted is believed to be a fairly accurate estimate of the population in the study area. Condors sometimes roosted on Isla San Gallan, but they were not censused since this island was not included in the study area. Few condors ever left their roost ledges before the census period ended. Black and white adults were quite conspicuous against the brown rock. Color of the immature birds blended with the background, so they were often difficult to see. Although we may have missed a few young condors, I was able to minimize the effect of this bias with a correction factor, using the number of observations of immature birds and adults made that month. Adjusted totals given in Table 57 vary little from the total number of condors censused, partly because the less conspicuous, younger condors represented such a small fraction of populations in the Paracas area.

I estimated the condor population size in August 1969 using data from a periodic roost census. I observed 9 and 10 condors on two trips to one roost in August. Using a mean value for

Table 57. Avian scavenger population levels on Isla Zárate and along 98.8 km of Peruvian coastline. Censused by boat from 0530 to 1030 in the morning during the second or third week of each month.

	No. counted in:						
	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
Condors							
Adult male	-	2	6	13	4	2	0
Adult female	-	4	9	14	4	3	1
Adults -sex unknown	-	6	1	10	13	17	22
Immature	-	0	2	1	0	1	0
Total	-	12	18	38	21	23	23
Correction factor[a]	-	(57/54)12	(128/124)16	(83/78)37	(130/120)21	(205/196)22	(124/119)23
Adjusted total	30[b]	13	18	39	23	23	24
Turkey vultures	-	-	75	92	81	41	53
Gulls (Peruvian and kelp)	-	-	315	449	604	482	301
Humans	-	2	30	5	11	14	7

[a] An estimate for the total population is made by adjusting the number of adults counted on the census with a ratio on the age distribution for condor observations made that month, a ratio of all-aged condors to adult condors.

[b] Extrapolated from data recorded periodically at an individual roost (see text).

the proportion of the population at that roost on eight other occasions, I extrapolated to secure a rough estimate of 30 condors frequenting the study area in August 1969. I assumed that the proportion of the population using the roost did not vary with time or with population size.

Population estimates for the smaller, less conspicuous, and more mobile turkey vultures are believed to be less accurate than estimates for the condor, whereas those for gulls should deviate significantly below actual levels. These census data for the smaller scavengers, gulls in particular, are quite useful as relative indices but are less so as absolute measures. Monthly estimates for the condor population varied from 13 to 39, while values for turkey vultures ranged from 41 to 92 and Peruvian and kelp gulls from 301 to 604. Humans counted on the beaches varied in number from 2 to 30.

Scavengers Supported On the Beach Stratum

From blinds placed on or near study area beaches I recorded the number of feeding minutes by vultures and gulls on different food species available there (Table 58) to secure estimates for the amount of each food type taken by the different scavenger species. Using mean rates of ingestion described earlier in this chapter, I converted values for feeding minutes to estimates of food mass consumed (Table 59). These computations provided a relative measure of the amount of each general food type (birds, mammals, others) consumed by each of the scavenger groups. Thus, an estimated 51 percent of the bird mass consumed on the beaches was taken by condors, 47 percent by turkey vultures, and 2 percent by the Peruvian and kelp gulls. For mammals, the estimate proportion taken by condors was 63 percent, for turkey vultures 35 percent, and 3 percent by gulls. Applying these relative measures to data from the food survey, I was able to obtain monthly estimates for the total amount consumed on beaches of the study area

Table 58. Number of feeding minutes by different avian scavengers distributed according to the kind of food. Data recorded from blinds along 22.2 km. of Peruvian beach from August 1969 to February 1970.

	Birds			Mammals		Others
	Guanay cormorant	Humboldt penguin	Peruvian diving petrel	Sea lion	Burmeister's porpoise	
No. baits observed	8	8	3	16	10	2 [a]
Total no. min baits observed	1,540.0	440.0	120.0	5,155.0	3,845.0	270.0
Condors						
No. min one or more present	0.0	135.0	0.0	452.0	69.0	0.0
Total no. feeding min	0.0	146.0	0.0	560.0	69.0	0.0
Turkey vultures						
No. min one or more present	297.5	283.5	37.5	694.0	381.0	60.5
Total no. feeding min	310.5	290.5	37.5	1,096.0	534.0	60.5
Peruvian and kelp gulls						
No. min one or more present	63.0	1.5	0.0	14.5	269.0	13.0
Total no. feeding min	64.0	1.5	0.0	24.5	279.0	13.0

[a] Fish were observed in both instances.

Table 59. Estimates for the proportion of three classes of carrion taken by the different scavenger species in the Paracas study area.

Scavenger species	(a) Estimated rates of ingestion in g/min. (p)	(b) Number of feeding min. observed at blinds (Table 58)			(ab) Estimates for amount consumed in g			Percent of food mass consumed by the different scavenger species		
		Birds	Mammals	Others	Birds	Mammals	Others	Birds	Mammals	Others
Condors	47	146.0	629.0	0	6,860	29,560	0	51	63	0
Turkey vultures	10	638.5	1,630.0	60.5	6,380	16,300	600	47	35	92
Gulls (Peruvian and kelp)	4	65.5	303.5	13.0	260	1,210	50	2	3	8

by condor, turkey vulture, and gull populations of the coast (Table 60). For example, of an estimated 49.450 g of bird flesh consumed in August on the sample beaches (Table 53), an estimated 51 percent (Table 59), or 25,270 g, was taken by condors.

Finally, estimates for the unit number of scavengers supported by the beach stratum of the study area were secured by dividing values for food mass consumed by one individual into these monthly estimates of biomass consumed on the beaches (Table 61). So, for example, an estimated 25,440 g consumed by condors in one week (Table 60) represents the estimated amount consumed by eight individuals in one week, assuming a condor consumes 480 g per day (Table 56). 25,440 g/week/(480 g/day/condor) (7 days/week) = 8 condors.

I also assumed that the proportion of the three food classes taken by each type of scavenger did not vary from month to month. Data on the number of scavenger-feeding minutes was recorded throughout the period of study and only from observations of food items that appeared on beaches of the study area. If food items were observed in exact proportion to their presence on the beaches, the percentage of feeding time for each scavenger species would probably approximate the values obtained for diet composition in Figure 30. In this part of the study, however, we were not measuring the fraction represented by the three major groups in the diet of each scavenger, but rather how each of the three food groups were split among the scavengers. Hence, items of each food group, mammals for instance, were observed from blinds until we had representative values for the amount of feeding time by each scavenger group.

Although the relative measures of food consumed by different species should provide good estimates of these mean conditions, more accurate assessments for each month would require monthly means for the number of scavenger feeding minutes. Reliable estimates of food

Table 60. Estimates for the biomass of birds, mammals, and fish consumed per week on 22.2 km. of Peruvian beach by the three types of avian scavenger. Estimates for the total amount of biomass consumed per week on study area beaches from Table 53 are broken down according to the estimated amount consumed by each scavenger species using the percent values given in Table 59.

Scavenger species	Food class	Estimates for mass consumed (g) in: Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
Condors								
	Birds	25,270	8,350	0	1,970	0	10,080	2,490
	Mammals	170	760	15,750	940	0	2,370	1,890
	Others	0	0	0	0	0	0	0
	Total	25,440	9,110	15,750	2,910	0	12,450	4,380
Turkey vultures								
	Birds	23,280	7,690	0	1,820	0	9,290	2,300
	Mammals	90	420	8,750	520	0	1,320	1,050
	Others	0	0	0	280	2,070	170	6,110
	Total	23,370	8,110	8,750	2,620	2,070	10,780	9,460
Gulls (Peruvian and kelp)	Birds	990	330	0	80	0	400	100
	Mammals	10	40	750	40	0	110	90
	Others	0	0	0	20	180	20	530
	Total	1,000	370	750	140	180	530	720

Table 61. Estimates for the number of avian scavengers supported by food taken on 22.2 km. of Peruvian beach. The estimated number of scavengers supported was calculated by dividing estimates for food consumed by the scavengers from Table 60 with estimates for the amount consumed per bird from Table 56.

	Estimated unit no. individuals supported on study beaches						
Scavengers	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
Condors (a)	8(6,11[a])	3(2,4)	5(4,7)	1(1,1)	0(0,0)	4(3,5)	1(1,2)
(b)[b]	7	2	4	1	0	9	1
Turkey vultures	10(8,15)	4(3,5)	4(3,6)	1(1,2)	1(1,1)	5(4,7)	4(3,6)
Gulls (Peruvian and kelp)	1(1,2)	0(0,1)	1(1,1)	0(0,0)	0(0,0)	1(0,1)	1(1,1)

[a] Upper and lower bound estimates in parentheses obtained using confidence limit values for the mean daily food mass consumed (Table 56).

[b] Estimates for condors (b) obtained using data on food mass consumed per bird from crop observations (see Table 63 and p. 265).

portioning on a monthly basis could be secured only with a considerable increase in the amount of observation time from blinds, which would approach the extreme but ideal condition in which every beach is watched every day. Because only food occurring naturally was observed, however, errors due to monthly variation in food portioning should be minimal. For example, data on the relative feeding pressures for birds as food were recorded during periods when dead birds were abundant, so values obtained should be appropriate for those months when the biomass of birds consumed was high.

Monthly estimates for the proportion of the condor population censused on the study area (Table 57) supported by the open beach stratum (from Table 61) ranged from zero in December to 27 percent in August. The fluctuations are considered in detail in the following section. Beach foraging appeared to be more important for vultures than for gulls; the median of monthly values for the fraction of the population supported on food taken from the beaches were 1 of 5 for condors, 1 of 20 for turkey vultures, and 1 of 500 for the gulls. Differences between monthly estimates for the two species of vulture were not significant, but, combined, these values were significantly greater than those for the gulls.[7]

Using another method for estimating the amount of food mass consumed by condors (see p. 236-237), I secured a median value of one out of seven condors provided for by food on the beaches. Tests of differences in comparisons with the ratios of gulls and turkey vultures gave the same results obtained above. When the values of Prather *et al*. (1976) are substituted in place of those I obtained for food mass consumed daily by turkey vultures, the estimate of turkey vultures supported on the beach stratum increases to 1 of 8. The majority of vultures were apparently being supported by food taken on the short, rocky shores beneath sea cliffs. There, they could

feed without danger of human disturbance (Table 57, note the number of humans observed on study beaches during the census hours).

Errors in the census probably underestimate sizes of the total gull population, so the actual fraction of the population supported on the beaches was probably even lower than those computed in this study. The fraction of gulls supported there was quite small, probably because these birds were exposed to food on or near the surface of the water in addition to that washed ashore. Proportions of food type obtained (Figure 30) suggest that most of their food was taken from the water; it is unlikely that a cliff-to-beach preference by feeding gulls would account for the small fractions I obtained.

Some of the food partitioning on beaches between scavenger species might have occurred on a temporal basis. Differences were significant in the frequency of feeding occurrences observed between turkey vultures and condors according to the time of day (Table 62).[8] In the major departures, condors fed relatively more often from 0900 to 1000, whereas turkey vultures preferred the period 0600 to 0700. Although coastal condors did show a preference for feeding during the early morning periods around 0700 (p. 207), the preference was less marked than that of the turkey vulture. The relatively greater mobility of the smaller vulture probably guarantees earlier feeding. The large size of the condor is linked with a lower metabolic rate, so condors may not have to feed as frequently as turkey vultures, regardless of the time of day.

Monthly Variation in the Relationships Between Condors and Food

Crop contents. Values for food mass consumed by the captive condor could deviate from actual amounts taken by free individuals. Wild condors might consume more food to power the additional activities that free-ranging conditions involve. On the other hand, when food is

Table 62. Feeding time for condors and turkey vultures on the Paracas study area. Recorded from August 1969 to February 1970.

		Percent feeding occurrences observed during period listed								
	No. Observ.	0600-0659	0700-0759	0800-0859	0900-0959	1000-1059	1100-1159	1200-1259	1300-1359	1600-2000
Condors	68	0	18	13	41	6	6	1	9	6
Turkey vultures	140	11	18	20	12	16	9	2	6	4

difficult to obtain, wild condors probably survive on less than that taken by a captive bird; I did not attempt to determine minimum food mass requirements with the captive condor. Observations on the crop contents of wild condors provided a means for estimating the amount actually consumed by these birds (Table 63).

Eight categories were distinguishable. Estimates of the mass contained for each category were determined by feeding measured amounts to the captive bird. In Africa, Houston (1976) used the same technique to estimate the amount of food taken by griffon vultures. In this study, the number of observations on condor crop contents was large enough to allow monthly estimates. Monthly differences of observations of crop content were significant, considering the months of August to February and gathering crop content categories of 81 to 800 g.[9] Mean estimates for the biomass carried in the crop varied from 120 g in January to 480 g for February, with a median of 320 g in August.

Assuming (1) that the profile for the amount of biomass carried by crops of the condor population was constant during the second and third week of each month (the census period), and (2) that observations on crop contents for the full month reflected that profile, I was able to estimate the food intake by the population from its crop-emptying rate (Table 64). Assuming that the emptying rate was constant for all hours of the day and for crops of varying contents, the feeding rate of the population should equal the emptying rate of the population. At night, condors could digest food but probably did not ingest any; this restriction on feeding time should not affect the analysis, as long as the distribution of the crop contents observed reflected the average actual distribution for the day. To get monthly estimates for the mean biomass consumed per day by each condor, I multiplied the percent of condors observed with food-laden

Table 63. Record of crop contents for condors observed along a 98.8 km. coastline study area in Peru. April 1969 to February 1970.

	Percent of crops observed with the contents (*g*) listed:								Total No. Observations	Estimated mean food biomass carried/condor (*g*)
	0-80	81-200	201-300	301-400	401-500	501-700	701-800	801-1500		
April	80	1	10	0	3	0	3	4	79	130
July	77	0	0	2	4	0	2	15	48	240
August	55	0	0	16	6	5	4	14	85	320
September	44	7	2	2	19	0	0	26	57	430
October	47	6	1	5	5	8	2	27	128	440
November	49	7	0	2	6	2	0	33	83	450
December	72	12	3	2	4	3	1	2	130	130
January	82	4	1	5	1	2	0	4	205	120
February	46	3	0	8	4	6	1	31	124	480

Table 64. Estimates of biomass consumed per week by a condor population living along 98.8 km. of Peruvian coastline. Figures are derived from data on crop contents of free condors and crop-emptying rates of a captive condor. August 1969 to February 1970.

Month	(a) No. condors on study area (Table 57)	(b) Percent of condors observed with food-laden crops (Table 63)[a]	(ab) Estimated average no. condors with food-laden crops at any one time	(ab) Crop emptying rate/week Estimated amount consumed/week by condor population			(b) (Crop emptying rate/day) Estimated amount consumed/condor/day
				Mean	95 percent confidence intervals[b]		
August	30	45	14	110,000	60,000	160,000	500
September	13	56	7	50,000	30,000	80,000	600
October	18	53	10	80,000	40,000	110,000	600
November	39	51	20	150,000	80,000	230,000	600
December	23	28	6	50,000	20,000	70,000	300
January	23	18	4	30,000	20,000	50,000	200
February	24	54	13	100,000	50,000	150,000	600

[a] All crops in the 0-80g category assumed to be empty. For the precision indicated, figures for the daily amount consumed per condor remain unchanged even if 5 percent of the condors observed with stage-1 crops were considered to be carrying food.

[b] Confidence intervals from variation in crop emptying rate (p. 259).

crops each month (Table 63) by the crop emptying rate per day [(46 g/hr) (24 hr/day), pp. 230-231]. Hence, in Table 64, for August, an estimate of 500 g consumed per condor per day was obtained by multiplying 45 percent (the proportion of the population carrying food) by 1104 g per day, the mean crop-emptying rate per day.

Profiles for the amount of biomass carried in crops of the condor population changed from month to month. The effect of these month-to-month changes altered mean estimates for the daily biomass consumed per condor each month by amounts all less than four percent. Values for mean and confidence interval estimates in Table 64 are rounded, so the precision indicated allows for any errors of that magnitude.

Values for the estimated mean food biomass in the crop of each condor (Table 63) vary from month to month in a slightly different fashion than do the values for the estimated amount consumed per condor (Table 64), because computations of the latter consider only the fraction of condors with food-laden crops; whereas in the former, figures are obtained using observations on crops of all condors observed. Monthly estimates of the two quantities remain in an exact ratio with one another only if month-to-month distributions of the biomass carried in laden crops remain constant.

Although the mean monthly estimate for the daily amount consumed per condor was nearly the same as that obtained with the captive bird (500g, 480g, respectively), monthly variation around that mean was marked, ranging from 200 g to 600 g. I secured new estimates for the unit number of condors provided for with food on the beach stratum by substituting the revised monthly estimates for the amount consumed per condor into the treatment outlined in Table 61 (condors b).

General comparisons. Monthly fluctuations of four major parameters describing condor populations and the food supply are graphed in Figure 31. Relationships between these variables can be examined by considering changes from one month to the next. Except for the one transition between August and September, clear and direct relationships between the study area population of condors and its food supply seem evident. The condor population within the study area apparently declined from August to September, while the amount of food available on the beaches and the biomass consumed per bird increased. A large supply of food may have existed just outside of the study area, perhaps along the rugged coast area to the south, and condors might have congregated there temporarily.

In October, the condor population increased slightly and so did the biomass of food sampled on the beaches. Crop observations indicated that individual condors continued to consume relatively large amounts. In October, sea lions began to concentrate on Isla Zárate and beneath the cliffs of the Paracas Peninsula to mate and give birth to young. From the mainland, I was usually able to note the relative amount of sea lion carrion available on the island. Monthly fluctuations were marked and probably represented critical periods that affected all of the sea lions in that area.

A number of profound changes occurred in feeding conditions for the condor in the three months following October. Feeding activity at Isla Zárate reached a peak in November. Dead sea lions there and on the Paracas Peninsula apparently provided the large amounts of biomass consumed by a population of condors that had more than doubled in number from the month before. Little food was available then on the mainland beaches, and only a slight fraction of the population was getting any food there. In December, food on the sample beaches disappeared

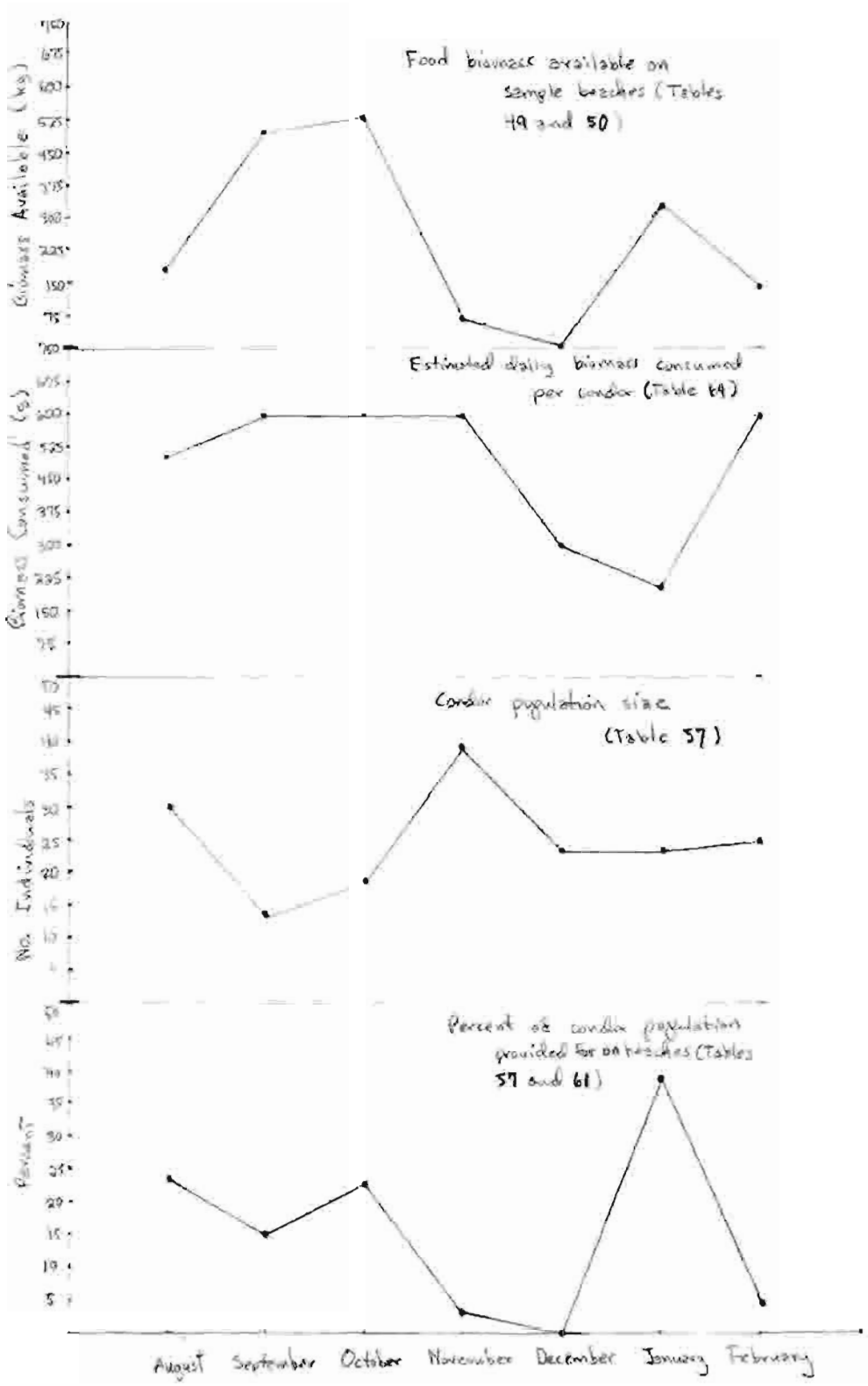


Figure 31. Monthly variation in four conditions relating condor populations to the food supply. August 1969 to February 1970.

and, although sea lions remained in large numbers on Isla Zárate, mortality on the island dropped considerably. In five days of island observation, I saw only two dead sea lions, both small animals each about 5 kg in mass. Biomass consumed per condor declined, as well as the number of condors on the study area. In January, the population remained unchanged, but the amount of food consumed per individual continued to drop. Food was once again available on beaches, and condors apparently were forced to feed there. Exposed beaches on the mainland did not appear to be preferred feeding locations for condors; the largest fraction of the population provided for with food taken on beaches (39 percent) occurred in lean times, when the daily food mass consumed per individual was a minimum during the study period (200 g). Comparative data on the alertness of birds feeding on the mainland beaches and Isla Zárate support this hypothesis of location preference (p. 217). In February, dead sea lions appeared daily on the island once more; crop observations indicated that condors again consumed relatively large amounts per individual, and mainland beaches resumed their relatively unimportant role as feeding sites.

In sum, condors fed on both birds and mammals on mainland beaches but apparently preferred to feed on rugged isolated parts of the coast, where most of the food taken was probably sea lion. Condors probably concentrate all along the Peruvian and Chilean coast in areas where and when dead sea lions are abundant. At least 50 condors, the largest concentration I ever saw, appeared on Morro Quemado, an area south of Paracas, on 22 January 1970, several days after a bird island warden had killed a number of sea lions there.

Comparisons With Other Areas

Crop Contents

Observations on crop contents of free-ranging condors provide a unique means for evaluating the quality of one important factor defining the habitat. In a comparison of the three study area, condors were found to carry more food, on the average, in Colombia (390 g) than in the Peruvian areas (250g and 290 g) (Table 65). Differences for frequency of crop sizes observed are significant.[10] We recorded most of these values over extended periods, so temporal variation was not considered. Because the feeding conditions of any condor habitat change from week to week, a systematic evaluation should also consider short-term conditions. In Paracas, monthly mean estimates for crop content varied across a wide range, from 130 g in April 1969 to 480 g in February 1970 (Table 63). Data on Colombian birds were recorded from March to May 1970, a period when condors were frequently seen. During the dry season from July to September, condors were observed infrequently, an annual cycle according to people of that area. I made no record of crop contents during that time but expect that they were well below the average 390 g recorded during the spring months. The frequency of movements from one area to another is probably related inversely to the amount of food that the population is consuming.

Differences were insignificant in comparisons of crop contents for birds of different sex and age classes in both the Paracas and Cerro Illescas study areas (Table 66). For Colombian observations, however, I found that adult females tended to carry less food than adult males.[11] Tests for differences in sex- and age-class distributions of crop contents were performed on raw data. I combined crop categories of 81 to 800 g when sample sizes were small.

Sex and Age Class Ratios

Immature condors in the Paracas area represented an average of only seven percent of the population observed (Table 67). In contrast, six of an estimated 14 individuals, or 43 percent of

Table 65. Crop content observations in the three study areas.

Study area	Estimate for mean food biomass carried per bird (*g*)	Percent of crops observed with the contents (g) listed			Total no. observations
		0-80	81-800	801-1500	
Paracas	290	63	21	16	939
Cerro Illescas	250	44	47	9	57
Colombia	390	42	42	17	60

Table 66. Crop contents for condors of different sex and age classes in the three study areas.

	Estimate for mean food biomass carried per bird (*g*)	Percent of crops observed with the contents (*g*) listed								Total no. observations
		0-80	81-200	201-300	301-400	401-500	501-700	701-800	801-1500	
Paracas										
Male	270	65	4	3	5	5	3	1	15	423
Female	320	59	6	1	5	5	4	1	19	432
Adult	290	63	5	2	5	4	4	1	16	876
Immature	190	71	5	0	8	8	0	0	8	63
Cerro Illescas[a]										
Male	160	45	35	10	3	0	3	0	3	31
Female	300	46	17	0	12	0	12	0	12	24
Colombia[a]										
Male	430	26	5	11	18	11	5	8	16	38
Female	350	65	0	0	0	0	10	5	20	20

[a] Only two immature condors were seen in each study area during the period that crop contents were being observed.

the condors in the Colombia study area, were immature birds. The atacama desert, where thermal currents, typically, are weak, might act as a barrier that selectively filters younger, less proficient flyers from others traveling to distant feeding areas like the Paracas coast. Another, more frightening alternative is that the skewed age ratio reflects evidence of reproductive failure, possibly pesticide-induced. In monthly comparisons for Paracas, both sex and age class distributions deviated significantly from that expected (Table 67).[12] In major departures, more males were observed than expected in April, whereas immature condors were seen in comparatively larger numbers in August. I am unable to account for either trend.

CONCLUSIONS

In Colombia, condors fed on domestic animals that fell into the canyons, whereas dead sea birds and mammals represented most of the diet on Paracas. Both of these elements, feral domestic stock and sea animals, comprised the food of condors in the Cerro Illescas. Birds appeared to rank first and fish last as food preferences. Although I saw no instances of predation by the Andean condor, a few observations of both captive and wild birds and reports by other field workers indicate that the condor is predatory at times.

Condors probably locate much food by searching for it directly over a home range. Such a method seemed common in Colombia. In Paracas, however, one observation of many condors congregating at a carcass during a very short period indicated that condors follow the foraging activities of neighboring birds, either to (1) find food or (2) land when the presence of others confirms the safety of feeding there.

Feeding times and wind conditions are closely associated. In Colombia, condors tended

Table 67 Sex and age class ratios for condors observed on the Paracas coast during 9 months from April 1969 to February 1970.

Month	Sex ratio for adults		Age ratio	
	Percent males observed	Total no. observations	Percent immature birds observed	Total no. observations
April	70	71	4	79
July	36	42	12	48
August	57	68	20	85
September	50	54	5	57
October	43	119	4	128
November	58	72	6	83
December	47	120	8	130
January	45	190	4	205
February	49	119	4	124
Total		855		939
Mean	49		7	

to feed at the baits during a 3-hour period that began at 1000. Feeding tapered off after 1300. In Paracas, however, winds suitable for flight often came up several hours earlier and, accordingly, feeding progressed around 0700. Part of the earlier trend in Paracas may have been due to a tendency by these coastal birds to roost near food sources. Compared to turkey vultures, however, condors fed more often from 0900 to 1000, whereas turkey vultures fed more often from 0600 to 0700, a difference obtained, no doubt, because the smaller vulture can fly earlier. Approaches to food by condors are often rather prolonged, a wariness obviously human-induced.

Most observations of skin tearing at the baits in Colombia were by adult males. This male-specific tendency may be related to their larger size. Possibly such sexual differences foster a separation between mates at a particular carcass to reduce food competition, so that both birds can feed more rapidly and depart earlier. Adult females did show a relative preference for feeding in the head region of the baits and less preference for the shoulder, brisket, and axilla region. The latter was a favorite place for tearing the skin, so males were likely to feed there, particularly when the carcass was fresh. Sites torn open on horses and sea lions seemed to be chosen in part on the basis of skin thickness. Values for skin thickness on sites torn open by condors on one horse were usually less than 2 mm; values for other places on the carcass generally exceeded 2 mm.

Alertness at food was measured in two ways: (1) in the number of times a feeding bird paused to look up, and (2) the brevity of each feeding bout. I found that adults tended to be more alert than immature condors; gulls, turkey and black vultures as a group appeared intermediate between the two age classes of condors. The black vulture seemed less alert than the turkey vulture. Alertness as an absolute measure is not necessarily a species, sex-and-age class nor

individual characteristic, for I found that alertness measures varied according to the location of food. On Isla Zárate, condors were much less alert than on the mainland even though the same population was monitored in the two locations; the difference suggests that alertness as measured in this study was less a social response than a response to the possible presence of man.

Feeding visits and bouts at the Colombia baits were shorter for adults, particularly males, than for immature birds. Adult males, the dominant class, had priority of access to food, so they could land, feed, and depart without hesitation unless another adult male, a dominant one, was present. In Colombia a subordinate adult male probably did not land until the dominant bird departed. Prolonged visits, multiple feeding bouts, and reduced levels of alertness were all characteristic of immature birds. Young birds may be learning to recognize possible danger at feeding sites, so feeding efficiency and alertness may not yet vary from location to location as it does with adults. The development of maturity-related dominance would also parallel this ability to discriminate levels of risk at various locations for feeding. In sum, younger birds seem more vulnerable to human depredation at food, because they are at the carcasses longer, a result of their subordinance and less efficient feeding techniques, and because they tend to be less alert.

In a study of the feeding ecology of avian scavengers on the Paracas coast, I examined various feeding characteristics of condors, turkey vultures, and Peruvian and kelp gulls to interpret general feeding relations among these species and, in particular, to determine how monthly variation in the food supply affected the scavenger populations. During each of seven months, we surveyed three beaches on a daily basis for one week to estimate the amount of food both available and consumed by avian scavengers that month. I computed composition of the scavengers as the percent of sightings for each scavenger species feeding on a particular category

of food items. Of 68 sightings for condors, mammals represented 79 percent of the food items and birds the remaining 21 percent. In 140 turkey vulture sightings, the food source was a mammal in 56 percent of the instances and birds 32 percent. The food item was either fish or invertebrates in 67 percent of 220 gull sightings and human refuse in another 27 percent.

As the first step for computing the proportion of each food category being eaten by each kind of scavenger, I obtained estimates for rates of ingestion by weighing at item before and after feeding and recording the time fed. Wild condors ingested at rates of around 47 g per minute; for turkey vultures, the rate obtained was 10 g per minute and for the two gulls around 4 g per minute. Several other feeding characteristics had to be measured before I could estimate the number of each scavenger species supported by each kind of food. The mean rate of crop emptying for a captive male condor was found to be around 46 g per hour. For this condor, I also computed a mean value of 480 g as a measure of the food mass consumed per day. For a captive turkey vulture, the mean value was 330 g and for each of four gulls (two Peruvian and two kelp) the mean was 130 g daily.

After recording the number of minutes of feeding by each kind of scavenger on the beaches for each general food category ,I could compute the amount of food actually consumed for each class by using ingestion rates to translate feeding minutes to amount consumed. These values for amount consumed provided a relative measure for the part of each general food variety (birds, mammals, others) taken by each scavenger group. I applied these relative proportions to the estimates of food actually consumed on the beaches by avian scavengers (recorded in the food survey) to calculate estimates for the amount actually consumed by each kind of scavenger. Finally, into these values, I divided figures for the daily food mass consumed

each day by one member of each scavenger species to extract an estimate for the number of individual condors, turkey vultures, and gulls actually supported by food found on the beaches.

To evaluate the importance of the beach stratum as a feeding area for each of the scavenger species, we censused their populations along the coastal study area on a monthly basis and then calculated the estimated fraction of these populations actually supported by food consumed on the beaches. The medians of these monthly values differed markedly among the species. For condors, a median estimate of 1 of 5 was supported by food found on beaches; for turkey vultures, 1 of 10 (or 1 of 8 using feeding data on Virginia turkey vultures); and gulls, a probably maximum of 1 in 500. Data used in these analyses were highly variable; only the difference between the two vultures and the gulls was found to be statistically significant.

Considering characteristic differences in scavenger types, the turkey vulture seems to be more of a generalist than the condor; the smaller vulture takes a wider variety of food and in more equal proportions. This more generalist type of feeding by the smaller vultures may permit them a more sedentary existence. Large-scale migratory movements timed with periodic concentrations of food--breeding colonies of sea lions, for example--may not affect turkey vulture nor gull populations to the extent that it does populations of condors. Although turkey vultures are subordinate to the condor, they can fly and feed earlier than the condor and use food in closer proximity to humans. Smaller body size, with its higher metabolism rate, probably requires the turkey vulture to feed more regularly than the condor, however. The large condor can probably suffer fasting for many days without ill effect. Darwin (1845, p. 211) made note of this possibility when he was in Chile.

The Chileno countrymen assert that the condor will live, and retain its vigor, between five

> and six weeks without eating: I cannot answer for the truth of this, but it is a cruel experiment, which very likely has been tried.

Although condors seem less mobile than turkey vultures when flight conditions are poor, the ability to withstand such long periods without food and the dominance status that its size imparts must offset the relative disadvantage.

By recording the size of food-laden crops borne by condors sighted along the beach, I was able to get estimates for the daily amount actually consumed per individual. Monthly variation in these estimates ranged from 200 g to 600 g. To obtain revised estimates for the number of condors supported by the beach stratum I substituted these monthly values for the mean daily biomass consumed by a captive condor. These revised estimates should more accurately reflect actual feeding conditions, because wild condors are unlikely to consume, on a consistent basis, the same mean amount taken by a captive bird; perhaps wild birds take more food when possible, because they are more active and take less at other times when food is scarce.

During this August to February study, food was present on the beaches in largest amounts in September, October, and January and least amounts in November and December; dead sea lions on the island were scarce in December and January. In general, condors apparently preferred feeding beneath the rocky cliffs and on Isla Zárate, areas free of human disturbance, and used food available on beaches only when all food available had diminished. The largest proportion of the condor population supported by food on the beach stratum (39 percent in January) occurred only when the estimated amount consumed per condor was at a minimum level during the period of study (200 g per day). When dead sea lions were available in number on Isla Zárate, beaches became relatively unimportant as feeding sites (a negligible fraction of

the population, 0 to 3 percent, was supported by food from the beaches, then) and crops observed indicated that condors were consuming more once again (around 600 g consumed per condor per day).

Observations of crop contents on wild condors also provide a means for evaluating one aspect of habitat quality for the bird. A comparison of the mean estimate for crop contents observed in the three study areas indicated food was more easily obtained in Colombia during the period from April 1969 to February 1970 (390 g per condor) than in either Peruvian areas (250 g in the Cerro Illescas and 290 g in Paracas). Such measures are highly variable in time, however, so the full annual cycle should be considered for habitat comparisons; in Paracas, for example, crop contents varied from a mean of 130 g in April to 480 g in February.

Immature birds represented a much smaller fraction of the transient condor population in Paracas (an average of only 7 percent) than they did in Colombia where 43 percent (6 of 14 birds) were immature birds. Immature birds, as less experienced flyers, may not be able to cross the Atacama Desert as easily as adults. Thermal updraft conditions in this desert are poor and most cross-country flights are probably fueled with vertical currents produced when the strong south wind of that area strikes hills, cliffs and ridges and is deflected upwards. Compared to flight in areas of thermal uplift, flight in deflection currents that are variable, erratic, and lower in altitude would be a more demanding venture. Pesticide-induced anomalies must also be considered as a possible cause for the low ratio of young birds.

I need to acknowledge several weaknesses in this coast ecology study. First, some data are too patchy for statistical treatment (food availability, for instance, as represented by the presence or absence of a large sea lion). Second, longer-term measurements for food mass

consumed by captive gulls and turkey vultures would considerably refine the accuracy of estimates for what the beach stratum supports. Nevertheless, I believe the work above is useful for the framework of analysis it establishes and for the baseline data provided for the period of this study. In the case of imprecise values for daily food masses consumed, more accurate values secured in the future can easily be substituted.

CHAPTER 8 FLIGHT

INTRODUCTION

How, when, and why do condors use the different major modes of flight like gliding, circling, of flapping? What other aerial maneuvers are employed, and for what purpose? How is flight affected by changing weather? The purpose of this chapter is to provide an understanding of how condors fly. The first sections of this chapter deal with gliding, flapping, and circling patterns. An analysis of other flight maneuvers like double-dipping, arching, and lowering the feet follows. In the last section, I consider how condor flight is influenced by topography and weather.

Andean condors are superb subjects for the study of bird flight in nature. To fly, these big birds depend on updrafts that are strongest near cliff faces and canyon walls in many areas. From cliffside observation points, the qualitative aspects of flight by this large bird can be seen clearly at close range. Individual movements in flight are relatively slow compared to those of other birds. Quantitative treatments of condor flight were possible at sites along coastal foraging routes, where air movement was steady and easily monitored.

As with most current analyses of bird flight, sections of this study are fairly technical. To provide some background for readers unfamiliar with aerodynamics, I outline here a few basic relationships that are useful for interpreting the results of this study and aid in understanding how birds fly. Most of the review material that follows is taken from sources listed at the end of this section.

When the wing of a bird moves through the air, one force called drag (F_D) acts in the opposite direction to the line of motion, and another force called lift (F_L) acts upward, perpendicular to the line of motion. The resultant (R) of these two forces is equal to and acts in

the opposite direction of the weight of the bird (W) when the bird is in a state of equilibrium gliding, that is, gliding without either accelerating or decelerating (Figure 32).

In this study of flight, examination of the forces that act around a wing centers on drag, what it is and how it works. Lift is simply considered as the force generated upward due to a pressure difference, which results when a fluid moves over the top of an object more rapidly than below it. Drag is a more complicated matter. This force acts to retard motion of the wing or bird and is of two general sorts, parasite drag and induced drag. Parasite drag can be most easily imagined in a system where no lift is generated. First, a certain amount of drag occurs simply from the friction of air passing around the wing and, secondly, as the energy left behind in the eddies of air produced by the wing's passage. After an object moves through a fluid, a certain amount of turbulence occurs, and it is the energy drained to produce this activity that represents the form of parasite drag called pressure drag. Friction drag and pressure drag are the two components of parasite drag and neither are affected by the lift generated. However, the other major component of drag, induced drag, varies markedly according to the lift the wing produces.

Lift produced at the center of the span is greater than that at the tip because the low pressure and high pressure zones above and below the wing meet at the tip. A pressure gradient that diminishes toward the tip has an important effect on the state of the air's movement just after the wing's passage. Near the center of the span, at the rear of the wing, air has a tendency to move up a greater rate than it does in a similar position near the tip because of the difference in the pressure gradient. Imagine then, the net movement of air behind the wing as a sheet rolling upwards, but rolling upwards more rapidly toward the center of the wing than at the tip. The sheet then rolls into a cone; in a fluid, this spiralling flow is called a vortex current. Producing these vortex currents requires energy, the net loss of which is called induced drag.

The shape of a wing is an important factor in determining the effect of induced drag.

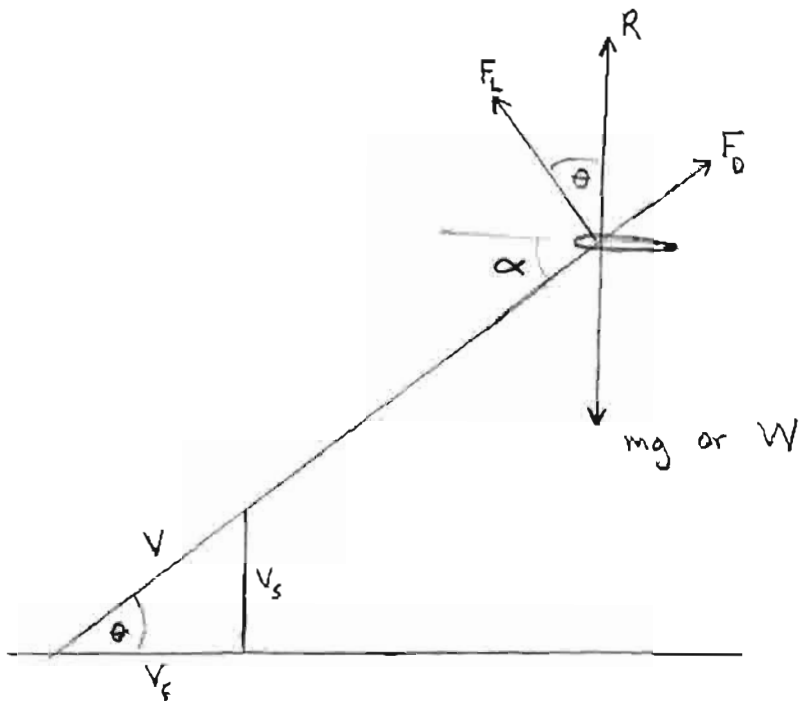


Figure 32. The relation between the glide angle and the forces of lift and drag.

Because vortex production is a tip effect, longer wings will produce more lift for a given amount of induced drag. For a given area of wing, then, relative length is an important characteristic and is described in terms of aspect ratio, the ratio of the wing's length to its width. Long narrow wings, those with a higher aspect ratio, usually can attain higher lift-drag ratios than short, wide wings.

The ratio of lift to drag determines the glide angle of the bird in a fairly simple and direct fashion. This relationship is illustrated in Figure 32. By varying the angle of attack (α)--that is, the angle between the wing and its direction of motion or the direction of the wind--the forces of lift and drag vary in strength but not in direction. For a given angle (α), the ratio of lift to drag is constant in a state of equilibrium gliding. The path of the bird can be considered as two components of its speed, the horizontal or forward speed (V_f) and sinking speed (V_s). The actual air speed (V) combines these two components so the glide angle of the bird (Θ) can be described as an angle with a tangent of V_s/V_f, or, more significantly, as an angle with a tangent that is the ratio of drag force to lift force (F_D/F_L). The angle Θ describes not only the glide angle but also the angle formed by vectors for lift and drag forces. In equilibrium gliding, the resultant force of lift and drag (R) is equal to the weight of the bird (W); hence, three equations useful in this study can be derived from the relations illustrated in Figure 32.

$$V_s = V \sin \Theta \quad (1)$$

$$F_D = W \sin \Theta \quad (2)$$

$$F_L = W \cos \Theta \quad (3)$$

Lift and drag are related in direct and similar fashion to a number of variables. Both forces are greater when the wing surface increases and when air is more dense. Air speed is a major factor; both forces are related to the square of the air speed. The following equations, conventional in aerodynamics studies, describe these relationships:

$$F_D = 1/2\ Sp\ V^2 C_{D'} \quad (4)$$

$$F_L = 1/2\ Sp\ V^2 C_{L'} \quad (5)$$

where C_D is the coefficient of drag, a composite of two other coefficients, C_{Dp}, the coefficient of parasite drag and C_{Di}, the coefficient of induced drag. C_L is the coefficient of light and describes the effect of such variables as the fluid viscosity of air, the profile and aspect ratio of the wings, and, especially, the angle of attack. The ratio of lift to drag, then, is the same as that of C_L to C_D, because all other variables determining lift and drag are the same for each force and cancel out in a ratio. Because the ratio of C_L to C_D or lift to drag is the same as that of forward air speed (V_f) to sinking air speed (V_s), the lift-drag ratio can also be described in terms of a glide ratio. For example, A C_L/C_D ratio of 10 is also a glide ratio of 10, which means that a bird gliding ahead 10 m/sec will descend at a rate of 1 m/sec so that the path of the bird descends 1 m for every 10 m of horizontal space traversed. In most studies of bird flight, the glide angles are small enough so that they can be considered as the full distance traveled over the distance dropped. In the computations of this study, as well, cos Θ was taken to be unity; variation from unity is negligible for the small glide angles considered here.

The weight-loading ratio of a bird is a ratio of its weight to wing area. Mean values given in Table 68 for the weight-loading ratio of condors vary from 85 newtons (N) per m^2 for an adult female to 102 N per m^2 for an adult male. For turkey vultures, the mean ratio for weight loading is 42 N per m^2. Substituting $\underline{W}\sin\Theta$ from equation 2 in place of F_D in equation 4 and solving for V, we find that air speed is directly related to the square root of the weight-loading ratio (W/S). In general, then, birds with a higher weight-loading ratio glide faster. Faster gliding speeds usually indicate higher sinking speeds, so soaring birds with high weight-loading ratios usually require strong vertical air currents to remain aloft without flapping. On the basis of weight-loading ratios, then, condors can be expected to glide more rapidly than turkey vultures

Table 68. Dimensions of the condor and turkey vulture.

	Unit	Condor		Turkey vulture[a]
		Adult male	Adult female	
Mass (m)	kg	11.7(4)	8.4(2)	1.98(4)
Wingspan (b)	m	2.99(7)	2.77(3)	1.79(3)
Wing chord (c)	m	0.38	0.35	0.26
Wing and intercepted body area (S)				
full extension	m^2	1.13	0.97	0.46
moderate flexion (span reduced 20 percent, Fig. 33)	m^2	0.95	0.82	--
Wetted area (S_w)				
full extension	m^2	--	--	1.06
tail open	m^2	2.70	2.37	--
tail closed	m^2	2.60	2.29	--
moderate flexion	m^2	2.23	1.99	--
Aspect ratio ($b^2/S = R$)	N/m^2	7.9	7.9	7.0
Wing loading (mg/S)	N/m^2	102	85	42

[a] Sexes similar in size.

[b] Mean value is computed from sample size listed in parentheses. Data from birds measured in the field are used with records taken from the following sources: Apolinar (1914), Murphy (1925), Poole (1938), Fisher (1946), Lint (1960), Conway (1962), and Olivares (1963).

and require more optimal air conditions for unpowered flight.

The effect of the wing's angle is very important in bird flight and deserves some additional comment. The angle of incidence described the angle between the wing and the long axis of the bird or airplane, whereas the angle of attack relates the wing to the wind. As the angle of attack increases, the coefficient of lift rises, up to a point. So, for a given air speed, lift increases as the wing tilts up, but only up to a certain point, the point of stalling. Stalling occurs when the smooth streamlined flow of air over a wing is disrupted, and turbulent eddies appear above and behind the wing. Lift drops dramatically when the wings reach a stalling point. The pattern of airflow around a wing affects not only the amount of lift generated but also the amount of drag.

To make a valid comparison for different airfoils, the airflow pattern must be considered. The pattern of airflow passing over the wing of an airplane will vary markedly from that passing over the wing of a smaller replica when air speed is the same. Performance values obtained for different airfoils should be considered according to certain airflow patterns. Flow conditions of any fluid around any object are described by the Reynolds number (Re), a dimensionless number that accounts for variability is viscosity effects. Reynolds numbers noted in this study were calculated with the equation

$$Re = Vc\ (p/u)$$

where c is the average length of the wing's chord (width of the wing) and u is the viscosity of the air. Both air viscosity (u) and density (p) are temperature- and pressure-related; in this study, the ratio p/u varied from 62,500 to 65,800. At similar Reynolds numbers, the pattern of airflow around two different wings is the same, even if they are moving at different speeds through air masses of different density and viscosity. In short, a given Reynolds number specifies a certain airflow pattern according to the chord length of the wing and the condition of the air.

Streamlines that are even and parallel at a relatively low Reynolds number describe a flow that is said to be laminar; at higher numbers, air molecules swirl between the layers, and this flow is said to be turbulent. This turbulent layer of lowing air, called a turbulent boundary layer, is not to be confused with the large-scale turbulence that occurs in stalling; here, the entire boundary layer pulls away from the airfoil and whirls in eddies.

Methods of classical aerodynamic theory are employed in this study of flight. For additional material on this approach, the reader is referred to Alexander (1968) and Cone (1963); for more technical analyses of flight and aerodynamics, see Prandtl and Tietjens (1934) and Scorer (1958). More recent works employ new theories of analysis such as the momentum jet theory and the vortex theory; for these, the reader is referred to Pennycuick (1975) and Rayner (1979).

A GLIDING FLIGHT

Method of Study

All data describing the aerodynamics of gliding flight were recorded at a Peruvian beach, Playa Chucho. This level beach is located about 30 km south of Pisco and 1 km east of the village of Laguna Grande. The beach extends 620 m east-west, separating a series of sandstone cliffs that ascend abruptly to 150 m on the west and slop gradually on the east end to 70 m. Before rising in a series of small hills, 5-15 m high, the beach stretches to the north into the desert as a flat for 300 m on the west end and 120 m on the east end. Condors flying along the coastline crossed the beach in straight smooth flight. At one end of the beach, they left declivity currents produced by the cliff-deflected south wind to encounter them again at the other end. This predictable flight path, together with the steady wind characteristic of that coast, provided an optimum setting for measuring parameters of condor gliding and flapping flight.

The observation segment of the beach was marked by two rock piles 60 c m in height and 250 m apart. I stood midway between them, and when a condor passed over each marker, I recorded the lateral distance to the nearest meter separating the flight path projected on to the beach from the marker. Libby Sale, posted 145 m north of and in line with the tower, recorded the angle of the bird's position above each marker using a sextant mounted on a swivel-head tripod. The sextant, a vertical scale with 80 2.5 mm divisions mounted on a horizontal base 58.5 cm in length, permitted angular measurements for computing values of altitude to the nearest meter. The tripod and sextant were adjusted so that, for each sighting, the base of the vertical scale was in line with the top of the marker. For each sighting, I used the angle tangent recorded with the sextant and the distance measured from the sextant to the flight path projected on to the beach to calculate the altitude of the bird. The distance traveled by the bird for each measurement varied according to the lateral displacement from the markers. I computed altitude and flight speed values in each case with adjustments for distance traveled. Considering possible errors in measurement of both angle and distance, I estimate each altitude value to be accurate within 3 percent. All estimates for accuracy follow criteria presented by Ku (1969).

The duration of the flight interval from one marker to the next was measured to the nearest 0.1 second with a stopwatch at the inland observation point. Simultaneously, changes in wind conditions were recorded on a series of gauges cabled from a 5 m tower standing near the center of the beach below the flight path. The tower supported a wind vane, a cup anemometer to measure horizontal currents, and a propeller anemometer sensitive to vertical currents. With data on the speeds of air and bird relative to the ground, I used the law of cosines in a vector analysis to compute values for the air speed of the bird. Measured values for the ground distance and time traveled are believed accurate within 2 percent, values for wind speed within 20 percent, and computed values for air speed of the condor within 4 percent.

Results and Discussion

For observations on 15 condors (11 males, 4 females) that crossed the beach without flapping during a 13-day period, the mean air speed and computed standard error were 15 ± 0.5 m/sec (Table 69). For 42 condors (23 males and 19 females) that flapped at some point while crossing the beach, the mean air speed and computed standard error were 14 ± 0.2 m/sec. As expected, five turkey vultures flapped and glided across comparatively slower at a mean rate of 10 ± 0.5 m/sec. The sine of the glide angle (O>>) was calculated by dividing the difference in altitude (i.e., descent or ascent) by the air distance traveled between the two markers. No vertical currents were ever detected by the propeller anemometer, I made no corrections for the distance of vertical movement recorded. Values of glide angle Θ computed for condors that did not flap ranged from a descent of 3.5^{o} to an ascent of 1^{o}. I computed sinking speed with equation 1. The mean sinking speed and computed standard error for the gliding condors were 0.5 ± 0.08 m/sec, and 0.4 ± 0.1 for the turkey vultures. Differences in air speeds and sinking speeds according to the sex of the condor were not significant.

Aerodynamic Relations

An analysis of the data on forward speeds and sinking speeds considering dimensions of the bird and properties of the air provide standard values useful in evaluating the gliding performance of the condor.

Size and weight values are listed in Table 68. The total weight of the bird depends to a large extent on the amount of food carried in the crop. The effect of this variable should have been negligible here, however, since crops were empty for 54 of the 57 observations made; only one bird had a full crop. Wing area (S) was determined by using a polar planimeter to measure the projected wing area from a photograph taken straight below a gliding condor and multiplying

Table 69. Flight data from measurements recorded at Playa Chucho. Each entry is a mean value followed by a computed standard error.

	Unit	Gliding condors (n=15)	Flapping condors (n=42)	Flapping turkey vultures (n=5)
Air speed (V)	m/sec	15 ± 0.5	14 ± 0.2	10 ± 0.5
Sinking speed (V_s)	m/sec	0.5 ± 0.08	0.3 ± 0.04	0.4 ± 0.1
Sine of glide angle θ	--	0.030 ± 0.005	--	--
Reynolds number ($x10^5$)(Re)	--	3.6 ± 0.13	3.3 ± 0.06[a]	1.7 ± 0.09[a]
Coefficient of lift (C_L)	--	0.7 ± 0.04	--	--
Total drag (F_D)	newtons	3 ± 0.6	--	--
Induced drag (F_{Di})	newtons	3 ± 0.2	4 ± 0.2	0.7 ± 0.07
Horizontal wind speed during observations	m/sec	5 ± 0.2	3 ± 0.2	2 ± 0.5
Initial altitude of flight path	m	60 ± 3	50 ± 2	30 ± 4

[a] Does not describe viscous flow regime for those moments during flapping.

it by the squared ratio of the actual wingspan to the wingspan of the projected image. For total wing area, I took the area of the plane projected by both wings together with that part of the body intercepted by straight lines joining the leading and trailing edges of the wing. Length of the average wing chord (*c*) was computed by dividing values for wing area by those of the span. The mean and standard error for lift coefficient calculated for the 15 gliding condors were 0.7 ± 0.04. As noted earlier, lift coefficients are dependent on wing shape and position and describe the effects produced by the angle of attack, the aspect ratio, the profile of the wings, and fluid viscosity of the air. In equilibrium gliding C_L is inversely related to air speed. Condors probably employed a narrow range of optimum speeds in crossing Playa Chucho; I was unable to obtain estimates for minimum and maximum limits for C_L. No doubt, the bird can fly more slowly than speeds recorded here, so lift coefficients can be higher, probably attaining values around 1.5 or 1.6 regularly (Pennycuick 1971a, p. 23).

Drag forces retard forward motion, and in an equilibrium gliding situation, the energy required to overcome these forces is equal to the loss of potential energy incurred in the descent through the glide angle (equation 2). I computed estimates for the two types of drag force, parasite and induced drag, using a procedure employed by Parrott (1970) in his wind tunnel analysis of black vulture flight. Induced drag, directly related to lift force is calculated with the equation

$$F_{Di} = \frac{F_L^2}{\pi \; 1/2 \text{ rho p}(bVM)^2}, \qquad (7)$$

where M^2 , the Munk span factor, accounts for non-elliptical distributions of lift across the wing. I used a span factor of 0.9, the same value used by Parrott for the black vulture. I obtained a

mean and computed standard error of 3 > 0.2 N (newtons) for induced drag forces for the gliding condors. Estimates for weight and size dimensions used in computing C_L and F_{Di} are considered accurate within 5 percent; values for C_L are believed accurate within 20 percent, and values for F_{Di} within 25 percent.

By subtracting the values for induced drag from those of total drag, estimates of parasite drag force (F_{Di}) were obtained. I computed coefficients of parasite drag (C_{Dp}) with the equation

$$C_{Dp} = \frac{F_{Dp}}{1/2 \text{ rho p} S_w V^2} \qquad (8)$$

where S^w is wetted or total surface area of the bird. Values for the wetted area were calculated with a technique devised by Tucker and Parrott (1970), whereby parts of the bird are equated with geometrical figures to secure surface area estimates believed accurate within 20 percent (Table 68).

Data recorded on five turkey vultures presented in Tables 68 and 69 have been treated like the data for condors, with one exception. I assumed that the general shapes of turkey vulture and black vulture were similar and estimated the wetted surface area of the turkey vulture by multiplying the value computed for the black vulture (Parrott, 1970) by the squared ratio of wing spans. Values for the wetted area of the condor determined by this method and the method mentioned above differed by only 1 percent; I expect the error for the turkey vulture estimate is equally insignificant, even though the profiles of the two smaller vultures do not seem very similar.

Information recorded on condors and turkey vultures that flapped at some time while crossing the observation section of the beach also provided estimates for the forces and coefficients of parasite drag. I corrected sinking speed values for these data, however, because

flapping rate and sinking speed are related (Figures 38 and 39). In an analysis of regression with flapping rate as the independent variable, I computed mean sinking speeds of 0.5 m/sec for condors and 0.6 m/sec for turkey vultures, for a projected flapping rate of zero.

The C_{Dp} values I obtained for gliding condors were implausibly low. With mean data on air speed and sinking speed, I computed a C_{Dp} of 0.001 for the gliding female condor; for the male, I obtained negative values for parasite drag forces, an impossible condition (Table 70). C_{Dp} estimates from mean data on flapping birds were also low. I calculated 95 percent confidence limits for the mean air speed and sinking speed observed and combined these upper and lower interval values to secure maximum and minimum estimates for the glide angle and, indirectly, the coefficients of parasite drag. So, for example, I divided the lower confidence interval value of 13.6 m/sec of the mean air speed into the upper confidence interval of 0.68 m/sec for sinking speed corrected for zero flapping, to calculate an maximum estimate for the glide angle of flapping condors. For these maximum angles, C_{Dp} estimates were 0.003 for the flapping male condor, 0.005 for the female, and 0.020 for the flapping turkey vulture. All C_{Dp} estimates for the condor are exceptionally low, either less than or within the range of optimum values defined for parallel airflow across a smooth flat plate (Table 70). Only the maximum estimate for the turkey vulture approximated values determined for the black vulture in Parrott's wind tunnel study. Apparently, some source of error has operated.

Sources of Error

I found that relatively small errors in the weight estimates for heavier birds produced substantial differences in the C_{Dp} values. In computing total drag, weight values of the first power were used compared to second-power figures for calculating induced drag. Thus, if the weight given for female condors is an overestimate of 1 kg or 12 percent, the C_{Dp} value for flapping female condors would figure as twice that shown. An error of similar proportions in the

Table 70. Estimates for the coefficient of parasite drag for condors and turkey vultures.

	Forward air speed (m/sec)	Sinking speed (m/sec)	Sinking speed adjusted for zero flapping (m/sec)	Sine of glide angle θ	Total drag force (N)		Induced drag force (N)		Coefficient of parasite drag	
					Male	Female	Male	Female	Male	Female
Mean data for sinking and air speed										
Gliding condors (n=15)	15	0.5	-	0.0333	3.8	2.7	3.9	2.4	-	0.001
Flapping condors (n=42)	14	-	0.5	0.0357	4.1	2.9	4.5	2.7	-	0.001
Flapping turkey vultures (n=5)	10	-	0.6	0.0600	1.2		0.7		0.008	
.95 confidence intervals for mean air and sinking speeds providing:										
(a) Minimum estimates for sin θ										
Gliding condors	16.4	0.29	-	0.0177	2.0	1.5	3.3	2.0	-	-
Flapping condors	14.5	-	0.32	0.0221	2.5	1.8	4.2	2.5	-	-
Flapping turkey vultures	11.8	-	0.38	0.0322	0.6		0.5		0.001	
(b) Maximum estimates for sin θ										
Gliding condors	14.4	0.63	-	0.0438	5.0	3.6	4.3	2.6	0.002	0.003
Flapping condors	13.6	-	0.68	0.0500	5.7	4.1	4.8	2.9	0.003	0.005
Flapping turkey vultures	8.4	-	0.82	0.0976	1.9		1.0		0.020	

C_{D_p} values for airflow parallel to a flat plate calculated for the following Re:	Turbulent flow (Prandtl equation)	Laminar flow (Blasius equation)
(1) 3.6×10^5, the mean Re computed for gliding condors	0.0054	0.0022
(2) 3.3×10^5, the mean Re computed for flapping condors	0.0055	0.0023
(3) 1.7×10^5, the mean Re computed for flapping turkey vultures	0.0064	0.0032

weight of the smaller turkey vulture changed the C_{Dp} by only 2 percent. This may help explain why data for the heavier condors, particularly the male, are more deviant.

Two other sources of error could account for the general trend toward low C_{Dp} values: (1) If a vertical wind component existed in the flight path area above the level of the anemometer tower, the values for glide angle Θ would be unduly low and would provide underestimates for the total drag as calculated with equation (2). (2) If the assumption of equilibrium gliding was unfounded and condors were decelerating during the period of observation, they could glide at angles less than possible in equilibrium situations. I found evidence that both sources contributed (McGahan, 1973a). A third possibility, where glide angle is reduced by an acceleration of wind acting in concert in inertial forces, is unlikely because the velocity of the even coast wind varied little if at all across the short span of the flight intervals.

Using a C_{Dp} value derived for the black vulture by Parrott (1970) and modified for the condor by the factor K (Tucker and Parrott, 1970), I calculated expected values for parasite drag (McGahan, 1973a). Forces computed with these data yielded corrected mean values for total drag of 3.6 N for flapping condors and 4.4 N for gliding condors (Table 71). According to the changes adjusted for drag, the mean glide of lift-drag ratio became 14 (a glide angle of 4^{o}), compared to the observed mean ratio of 33. In other words, a condor gliding with fully extended wings in still air normally will descend 1 m for every 14 m of lateral distance.

Flex-gliding

Description. Flex-gliding, a term from Hankin (1913), designates a gliding posture where the wings are partially flexed in the horizontal plane. In bending both writs and elbow, condors altered the wing configuration across a range from near full extension to some positions where the span was almost halved. Moderate flexion characterized smooth straight gliding journeys over long cross-country distances. Wing area is reduced by overlapping the primaries

Table 71. Values describing certain parameters of flight that are adjusted to satisfy a discrepancy in estimates of drag. Each entry is a mean value followed by a computed standard error.

	Unit	Gliding condors (n=15)	Flapping condors (n=42)	Flapping turkey (n=5)
Parasite drag (F_{Dp})	N	4.4 ± 0.3	3.6 ± 0.1	1.0 ± 0.1
Total drag (F_D)	N	7.7 ± 0.3	7.3 ± 0.2	1.7 ± 0.04
Sine of glide angle θ		0.073 ± 0.0005	0.073 ± 0.0005	0.087 ± 0.002
Vertical wind component	m/sec	0.7 ± 0.08	0.5 ± 0.04	0.3 ± 0.05
Deceleration	m^2/sec	0.4 ± 0.05	0.4 ± 0.03	0.3 ± 0.03

in flexing the manus and by relaxing the patagium in bending the elbow (Figure 33). Simultaneously, the tail usually contracts to a more closed position. Circling condors generally initiated long cross-country flex-glides with a dipping motion by both manus; then the wings and tail, which were expanded during the circling ascent, moved to the flexed position as the bird began the straight descending glide.

Many of these straight flights, uninterrupted by bouts of flapping or circling, extended over periods of 5 minutes. Recorded durations of four flex-glides were particularly long: 7 minutes 40 seconds, 9 minutes 42 seconds, 12 minutes, and 14 minutes 40 seconds. In the last observation, the condor, before disappearing in the distance, had traversed about 13 km ground distance and had lost only one-fourth of the 1000 m altitude gained in a circling bout prior to the flex-glide. If the bird continued to encounter the same air conditions he could have traveled 50 km in a period of about 35 minutes, a journey made possible by ascent in a circling bout only 8 minutes. During this particular observation, I was standing below the midpoint of the flight path described. Values for altitude were obtained by combining estimates of the angle of the bird's position above certain mountains or ridges with data from maps on the altitude of the landmark and its distance from the observation point. I was often able to determine the bird's position relative to the landmark by locating the bird's shadow on the ground and then using the sun's "line of sight" for triangulation.

Air speed. The forward air speeds of condors in a moderately flexed posture should exceed those of condors gliding with fully extended wings. In an equilibrium gliding system, a reduction of airfoil area coincides with an increase in velocity. I noted that the tails of condors crossing the observation beach at higher air speeds tended to be less expanded (Figure 34).

Assuming that the condor seeks to minimize sinking speed, velocity increases brought about by wing flexion can be computed with the equation

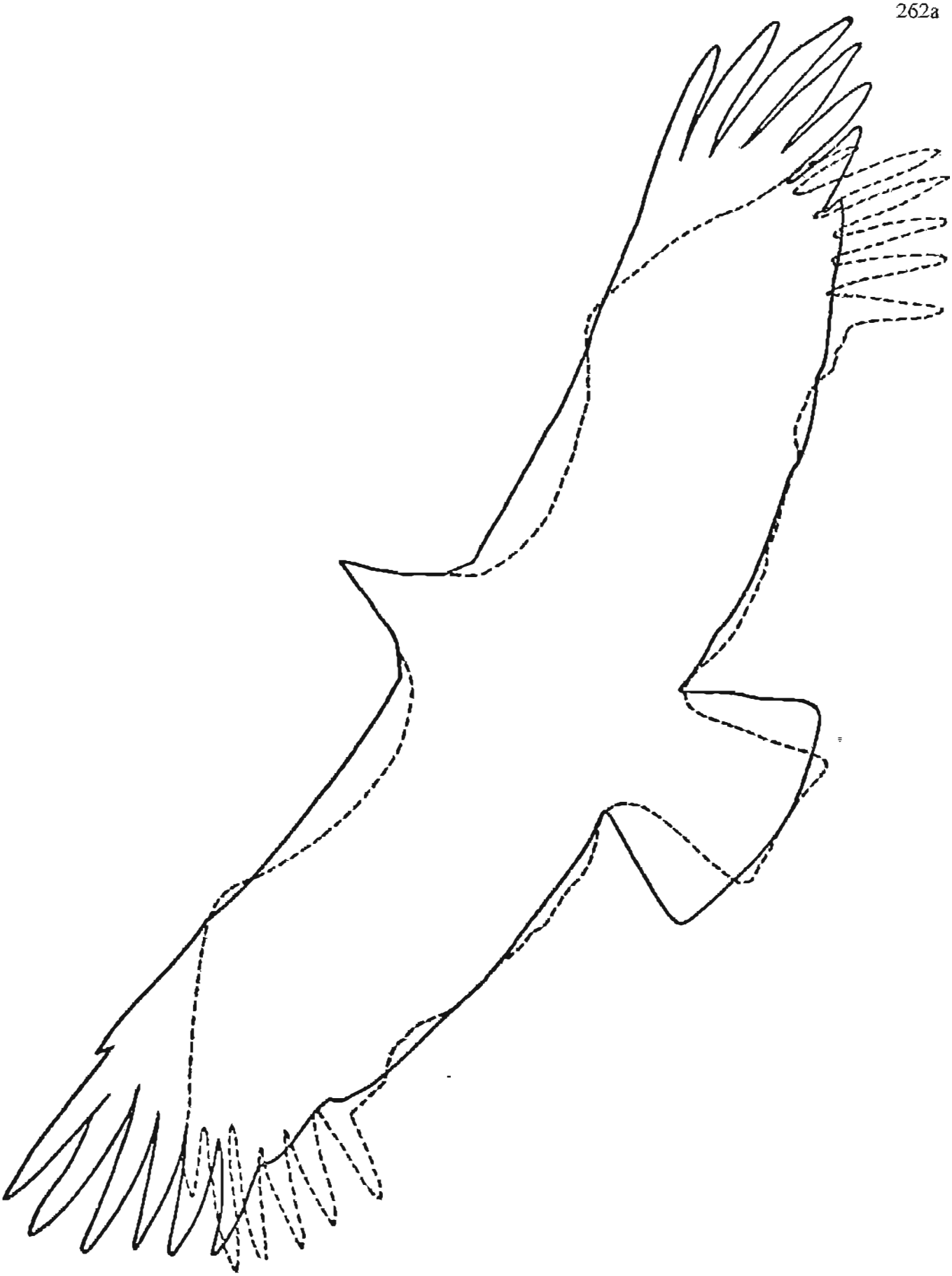


Figure 33. Differences in the flexed and extended gliding postures. Span in flexed posture is reduced by 20 perecent. Traced from photographs.

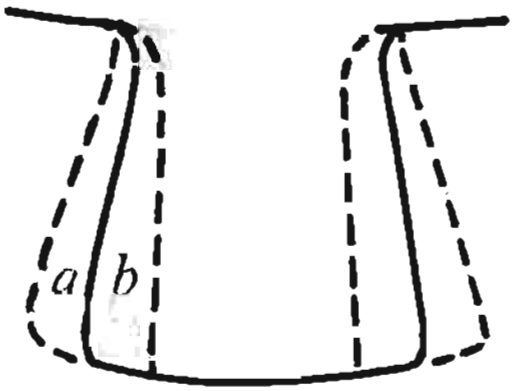


Figure 34. The degree of tail expansion related to air speed for 57 condors crosssing Playa Chucho.

$$S=2mg\ (M^2/\pi RC_{po})^{1/2}/\mathrm{rho}pV^2 \quad (9)$$

provided by Alexander (1968), where R is the aspect ratio and $C_{Do}=C_{Dp}\ S_w\ /\ S$, a parasite drag coefficient for wetted surface derived from the projected wing area. I used an air density value rho p=1.18kg/m^3, a parasite drag coefficient C_{Dp}=0.012, and the mean dimension values for male and female condors given in Table 68 to compute estimates for the air speed of condors in the two flight postures shown in Figure 33.

According to these computations, an adult male with wings fully extended would glide with minimum sinking speed when his forward air speed was 13.9 m/sec. Upon flexing them to the degree shown in Figure 33 (a span reduction of 20 percent), this optimum forward air speed would increase to 15.2 m/sec. Corresponding values for the adult female are 12.6 and 13.8 m/sec. These figures can serve only as rough estimates, however, C_{Dp} variation at different speeds is neglected, as well as airfoil effects of the tail.

Context and function. An ability to change forward air speed gives the condor flexibility for crossing areas with different kinds of air movement, food availability, and potential danger. Efficient increases in air speed are necessary for flight against a headwind; the condor must sacrifice the shallow glide angle of a moderate air speed for a speed that provides some forward progress relative to the ground. As air speed increases, the condor can minimize increased sinking speed by reducing airfoil area. I saw an adult female circling in a 40 km/hr wind flex her wing and tail more while traveling upwind than downwind, apparently accelerating upwind flight to reduce ground speed downwind. Five condors flushed from a cliffside roost circled up about 500 m above the sea and then, in postures flexed to the degree shown in Figure 33 (dotted line), glided in steep descent southeast along the coast heading against an evening cross wind of 30 km/hr. Ground speeds were noticeably reduced compared to those observed when wind speeds were less. Every 20-30 seconds, each bird flapped in a bout of three wing beats. Presumably,

these bouts served to reduce sinking speed and thus extended the potential endpoint of the descending flight path farther up the coast.

Frequently, condors flying in intense declivity winds near cliffs glided with strongly flexed wings and lowered feet. This posture occurred in flight patterns preceding landing, often during periods when the birds flew near my observation point and inspected me carefully. Fluttering wing covert feathers (Plate 27) and raised alulas indicate that the angle of attack with the steep vertical wind is large enough to detach part of the boundary layer of air moving over the wings. These stalling effects coincide with an increase in sinking speed and a reduction in forward speed. Lowered feet can function as air brakes to retard forward air speed. In an air mass that ascends rapidly, the bird is permitted greater sinking speeds without losing altitude; the reduction in forward speed can augment conditions for examining objects on the ground, enhance the precision of landing maneuvers, or provide prolonged access to local declivity currents of limited size. I watched an adult male advance with a fairly constant ground speed of only 0.5 m/sec for several minutes while flex-gliding near the edge of a cliff in a 35 km/hr headwind. Another adult male in a 30 km/hr headwind both advanced and ascended at the rate of 0.3 m/sec. One condor, flex-gliding in a defection current, maintained a high pitch angle of 35^{o} and climbed in steep almost vertical ascent without stalling. Sometimes, in strong deflection currents, condors with fully extended wings made little forward progress relative to the ground for extended periods; in one instance, a condor apparently gliding in the updrafts of a beach-deflected wind did not move, except for a gradual descent during a 40 second period. Then she glided downwind, ascended near the face of a bluff, and returned to assume this stationary glide above a carcass on the beach. Advancing slightly, another condor descended for 1 minute at a mean rate of 2.4 m/sec in a straight path that formed a 70^{o} angle with the ground. The wings were completely extended, and pitch was parallel to the horizon.

Increasing the weight-loading ratio of the airfoil by flexion may function at times to provide more stability for condors flying in turbulent updrafts. In pursuits and in flight patterns in restricted areas, temporary flexed-wing postures provided maneuverability. Acceleration forward and down succeeded wing flexion, and deceleration succeeded extension. Sometimes circling condors alternated between extended and flexed wing postures; in alternating between altitude gains and losses, they tended to remain in the same general area for extended periods. Eight times, an immature female alternately ascended and descended in a coastal declivity current. Flexing her wings to half span and simultaneously lowering her feet, she began a descent losing about 10 m altitude; then, extending her wings fully and lifting her feet back to the position against the body she initiated the ascent that carried her back to the original level. She did this while circling in the same general area.

Flapping Flight

Air movement around the flapping wing of a bird is strikingly complex; at every stage of the wingbeat cycle, the angle of attack and the strength of the relative wind are in flux and uniquely so for each spanwise section of the wing. The motor pattern of a wingbeat has been described in some detail, and mathematical models have been proposed (Cone, 1968; Weis-Fogh, 1972, 1973), yet few measurements have been recorded on the level, forward flight of flapping birds. This section presents a quantitative analysis of flapping flight by the condor.

Although condors flap infrequently when flying, the pattern does occur predictably in certain circumstances. On Playa Chucho, below one of their foraging routes I examined the effects of flapping on sinking and forward air speed. By combining these data with those taken from cine film of the wingbeat pattern, I was able to analyze in some detail the aerodynamics of flapping flight by the condor (McGahan, 1973b).

The procedure in measuring forward and sinking air speeds of condors crossing the observation beach has been described earlier. When condors flapped during the crossing, I recorded the number of wingbeats that occurred within the observation segment of the beach.

I filmed condors in flapping bouts from different positions with an 18-86 mm Switar lens on a Bolex 16 mm camera running at 64 frames/sec. I timed the duration of some flapping bouts to the nearest 0.1 second with a stopwatch.

The Wingbeat Motor Patterns

Condors usually flap when they take off and land. In level flight, they often flap when air movement has no upward component. Long flapping bouts are typical of chases among condors. Gliding condors may flap when they are suddenly alarmed. On the ground, they flap in apparent attempts to maintain balance while fighting, mating, or climbing up and down steep slopes. Adults flap their wings during courtship displays, during and after bathing and sometimes after sunning. Perched nestlings flap in begging displays and in long bouts that simulate flapping in flight.

The pattern usually occurs in short bouts. For level flight, I saw 175 bouts, of which 100 were composed of three wingbeats; two wingbeats occurred in only six bouts, four in 52, five in 16, and six wingbeats in only one bout, providing a mean and standard deviation of 3.5 ± 0.8 wingbeats per bout. No instance of a lone wingbeat was recorded for level flight; apparently, the efficiency of a single cycle is less for a given effort than a bout of flapping. In take off, wingbeat frequency is more variable and depends largely on the type of take-off site. For 11 instances of take off from cliffside perches, bouts varied from zero to eight wingbeats, with a median of two. Bouts for 21 instances of take off, all made downhill on a 30^{o} slope at a bait area, varied in extent from three to 23 wingbeats, with a median of eight. Bouts were significantly longer for take off from the more level site 1; apparently, the increase is necessary to attain a minimum air speed for

flight when immediate descent is not possible.

I recorded average durations of the wingbeat cycle in different activities (Table 72). A frequency of 1.8 cycles/sec, representative of normal level flight, for an adult female is less than the frequencies recorded for (1) three take off bouts that, in each case, began on the ground and ended after the bird was airborne (2.4, 2.8, and 3.0 cyc/sec), (2) an extended bout by a condor in escape flight (2.5 cyc/sec), and (3) a bout by a black vulture in level flight (3.9 cyc/sec) Frequency differences in the first comparison are probably due to a shorter cycle amplitude early in the take-off bout, which is necessary to prevent the wingtips striking the ground. Flapping sequences observed in courtship and copulation patterns on the ground were less rapid than those recorded for flight.

The Wingbeat in Level Flight

I recorded information describing wing movement in a frame-by-frame inspection of cine film taken of flying condors. When a condor in gliding flight begins to flap, the first movement carries the wings downward from the gliding position. At the onset of downward movement, the angle of incidence of the midwing area is reduced slightly, either by active rotation of the wing or by passive deflection of a less rigid trailing edge to the new angle of the resultant wind force. Near the end of the downstroke, the wing flexes slightly at the elbow and the wrist. The midwing section begins to rise before the primaries have completed the downstroke (Figure 35a, b, c; Figure 36). Once the primary tips reach the end of the downstroke, a nearly vertical position, the forearm and wrist section of the wing have already passed from their nadir below the body to a position level with it. The wrist and elbow remain partially flexed until the wing begins the downstroke (Figure 36d, e, f). The downward movement of the wing may act passively to extend the wing fully. The dihedral angle of the wings is about 45^{o} at the beginning of the downstroke (Figure 35e). When the flapping bout ceases, the gliding position is resumed,

Table 72. Wingbeat frequency recorded with a stopwatch to the nearest 0.1 sec.

Activity	Subject	No. wingbeats recorded in the bout	Mean no. cyc/sec
Normal take-off flapping both while running on the ground and after airborn	Immature male	9	3.0
	Adult male	9	2.8
	Adult male	10	2.4
Escape take off-all flapping while airborn (Table 74)	Subadult female	53	2.5
Level flight after take-off	Adult female	7	1.8
Level flight after take-off	Black vulture	7	3.9
Courtship display	Adult female	8	0.8
Copulation	Adult male	10	1.2
Exercise activity at nest-not airborn	nesting male	-	2.0

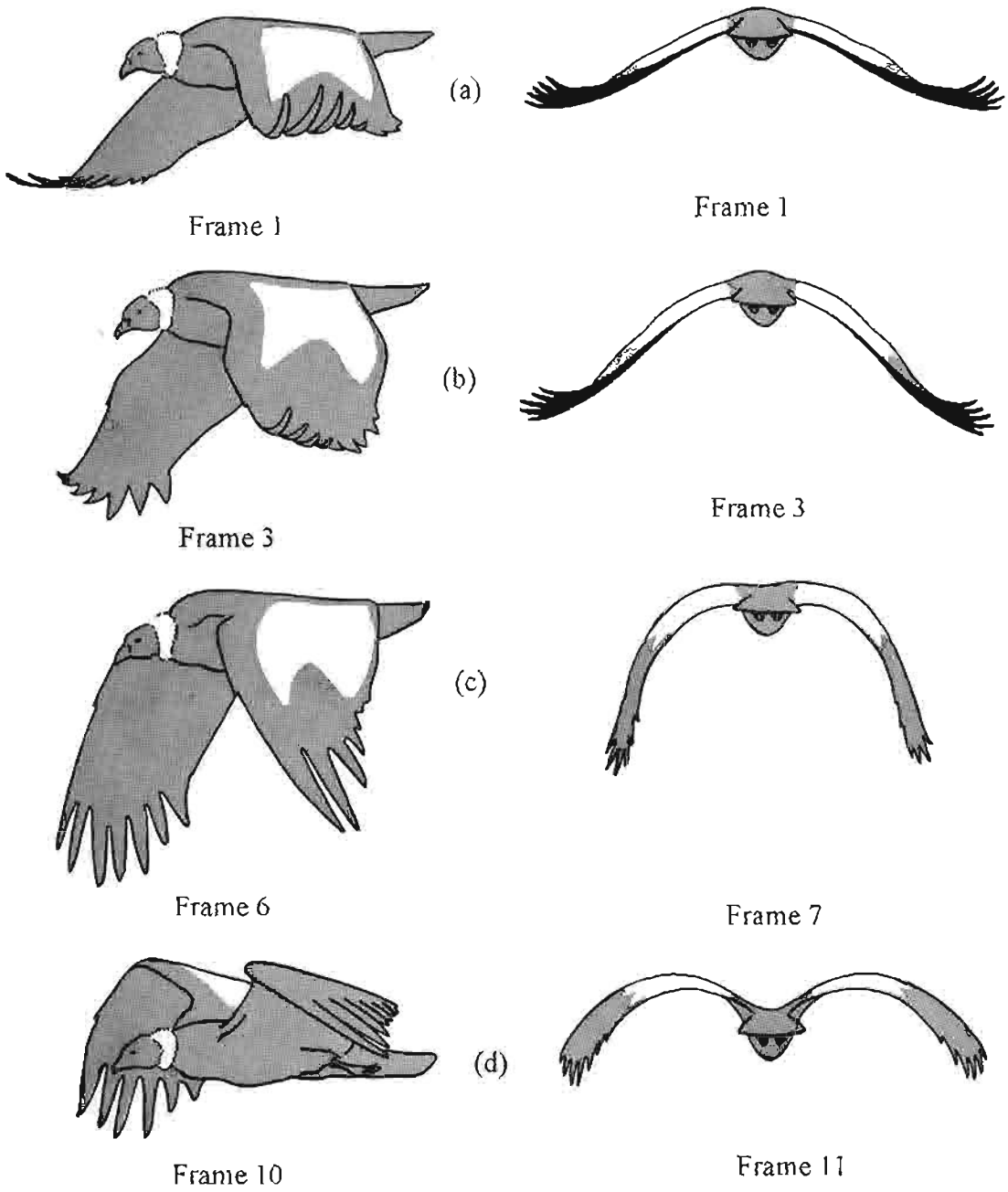


Figure 35a. Phases of a wingbeat cycle in level flight traced from cine film (64 frames per second).

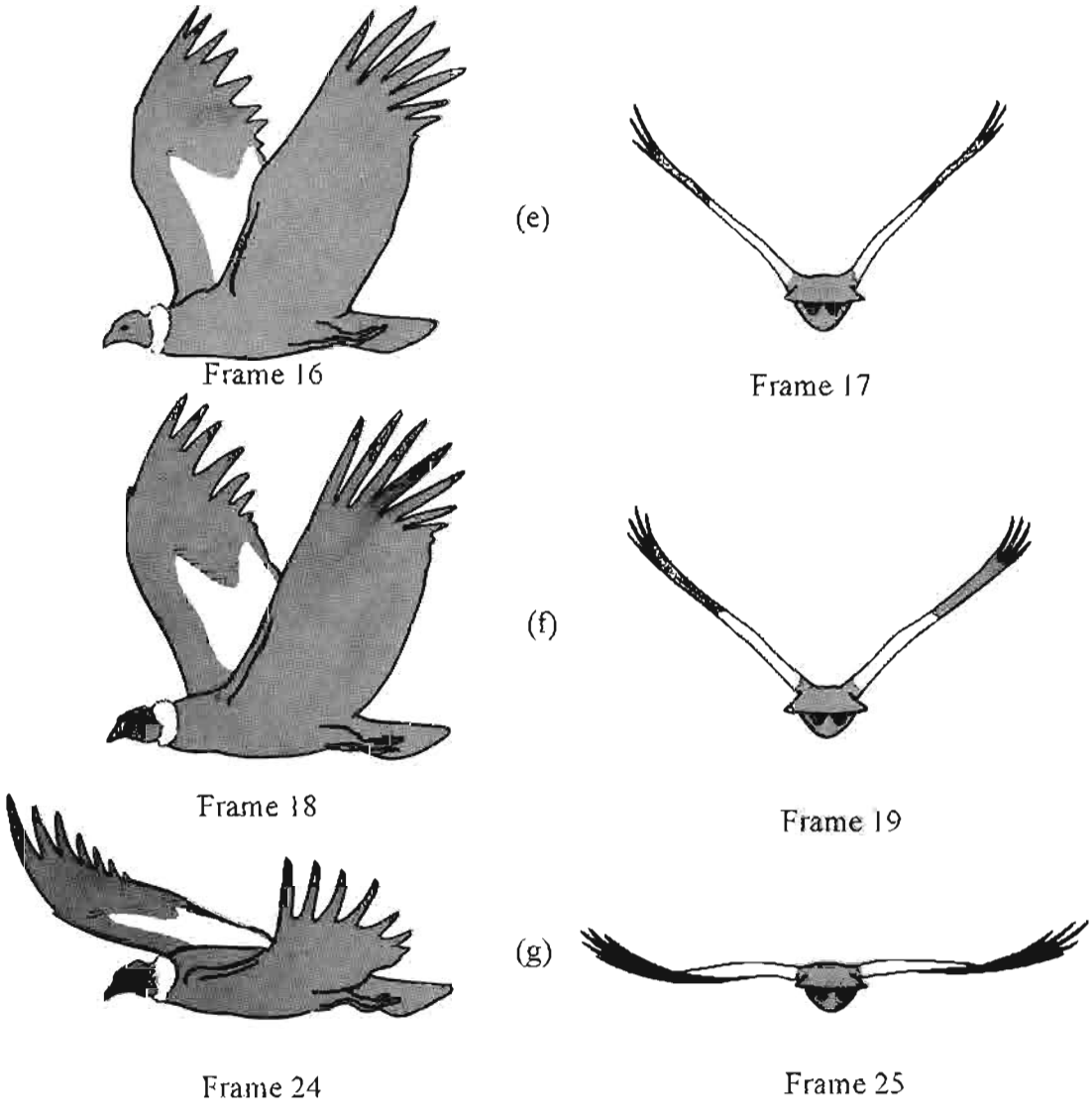


Figure 35b. Phases of a wingbeat cycle in level flight traced from cine film (64 frames per second).

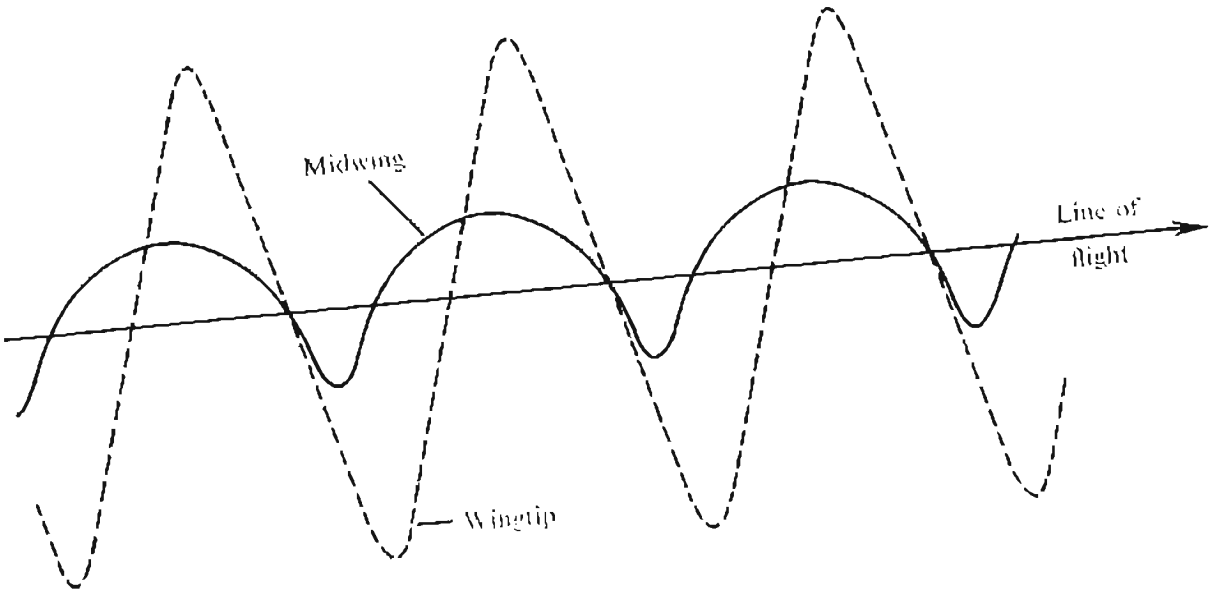


Figure 36. The relationship between midwing and wingtip phases of the wingbeat in level flight as represented by schematic paths of movement in lateral view.

with the upstroke terminating at body level. The half stroke that begins and ends a series of wingbeats seems no different from half the phase of a full stroke.

Relative durations of the upstroke and the downstroke vary along the length of the wing (Table 73). For an adult male in level flight the duration of the downstroke in the midwing area was approximately the same as that for the movement of the upstroke; at the wingtip, the downstroke required 61 percent of the cycle period and the upstroke only 39 percent. For a wounded adult male flying only 1-2 m above the sea, the upstroke duration at the wingtip was even more abbreviated, accounting for only 28 percent of the cycle period. The amplitude of the wingbeats seemed no less than that of a flap in normal flight; however, the wings did appear to flex more at the wrist and elbow on the upstroke. An immature male in take off also flapped with reduced upstroke durations at the wing tip. I could not clearly see mid-wing movement in the film segment on the wounded bird, but for the condor in take off, I found that the upstroke duration for that part of the wing was somewhat less than the downstroke duration.

The Wingbeat in Landing Flight

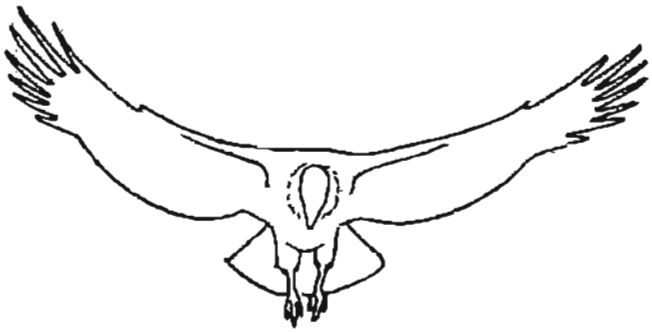
The wingbeat movement in take off appears similar to that of one in level flight, but the pattern in landing differs considerably. Flexion of the wrist and elbow is greater in the upstroke. The long axis of the wingtip path is oriented more in an anteroposterior than in a dorsoventral direction, and most of this path is restricted to a zone above the horizontal body plane (Figure 37a-g). Rotation of the path axis apparently serves to direct the wingbeat forces posteriorly to counteract the inertia of forward motion. Lift forces produced above the body support weight with a lower center of gravity and provide more stability than would occur if the forces were below or level with the bird. Also, in this higher position, the wings do not interfere with perch contact.

As the wings sweep forward in the downstroke, the pitch of the body increases, perhaps

Table 73. Relative durations of the upstroke and downstroke in the wingbeat cycle as recorded by cine.

		Percent of cycle period[a]			
		Midwing		Wingtip	
Activity	Subject	Downstroke	Upstroke	Downstroke	Upstroke
Level flight	Adult male	46	43	61	39
Level flight	Wounded adult male	-	-	72	28
Landing flight	Immature male	-	-	66	34
Landing flight	Adult male	-	-	64	36
Take-off flight	Immature male	51	38	70	30

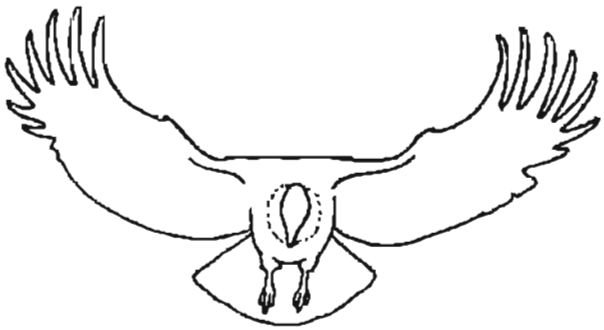
[a] Total for upstroke and downstroke does not equal 100 percent when there are pauses at the zenith and nadir of the cycle.



Frame 1

(a)

Frame 1



Frame 5

(b)

Frame 5

Frame 9

(c)

Frame 11

(d)

Figure 37a. Phases of a wingbeat cycle in landing flight traced from cine film (64 frames per second).

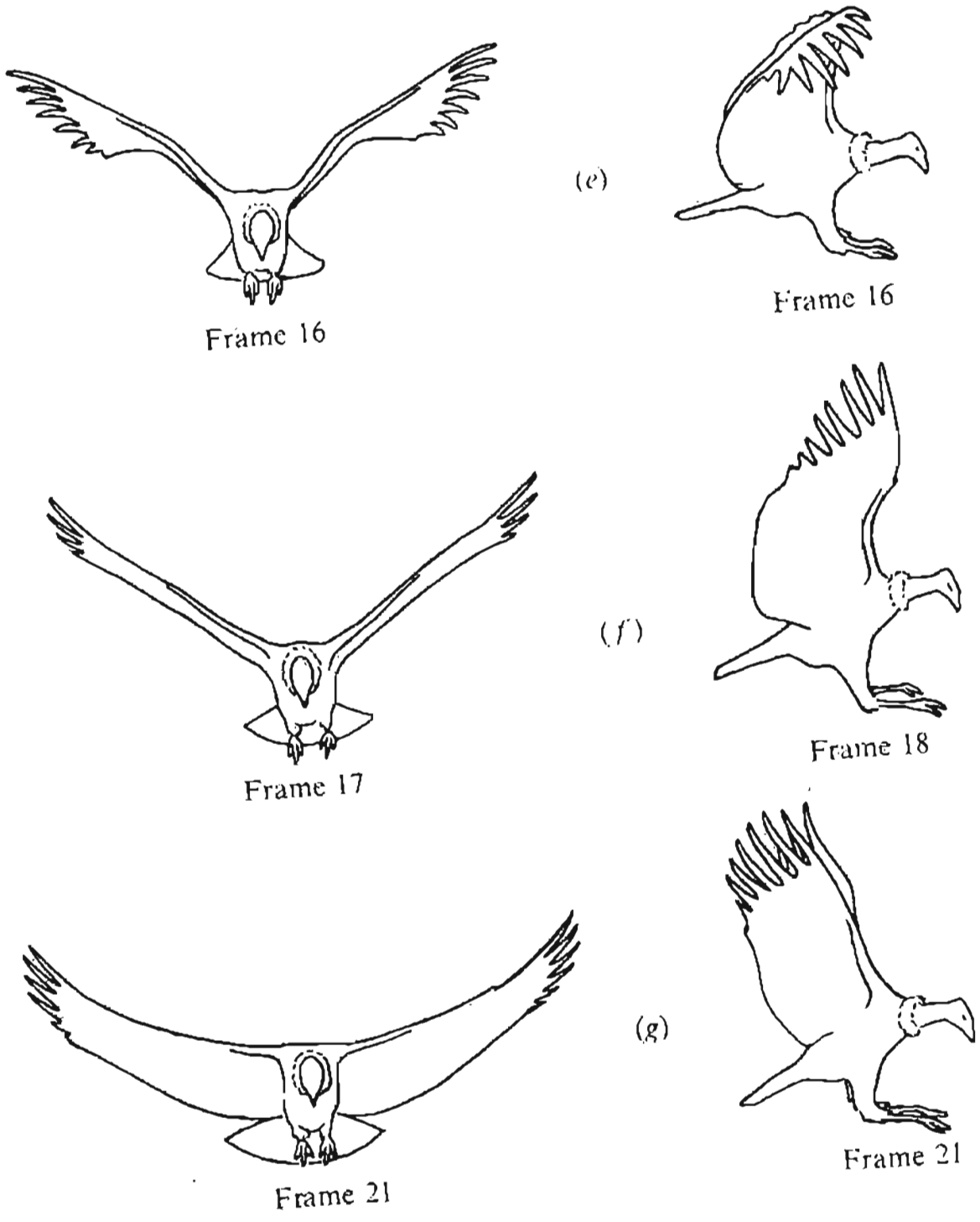


Figure 37b. Phases of a wingbeat cylce in landing flight traced from cine film (64 frames per second).

in response to the downstroke thrust (Figure 37c). During the succeeding upstroke, the pitch angle of the body decreases again (Figure 37e). As in level flight, the elbow and wrist flex to begin midwing recovery before the primaries have completed the downstroke (Figure 37b, c). The angle of incidence for the proximal half of the wing decreases rapidly and approaches zero as the primaries begin the upstroke (Figure 37d); near the end of the upstroke, the angle becomes negative (Figure 37e). The manus swings back and is extended, while the leading edge is rotated downward until the wing has about the same negative angle of incidence along the full length (Figure 37f). The downstroke begins, and the wings move forward and down, rotating at the same time to a positive angle of incidence. The alula rises in the downstroke (Figure 37a, b) and probably helps to retard boundary layer detachment by deflecting airflow downward over the midwing area. Coverts fluttering on the back of the proximal wing area and vibrating secondaries (Figure 37c) indicate, however, that stalling effects are present near the end of the downstroke.

To provide lift while landing, the wings in the downstroke compensate for the diminishing forward speed of the bird by increasing their angle of attack up to the stalling angle and by accelerating air speed across them through the flapping movement. Maximum lift forces are produced just before the boundary layer detaches in the stall. Apparently, lift potential is approached and then exceeded for different spanwise sections of the wing at different stages of the downstroke; the tip moves faster than the inner wing, so the effect moves distally. The condor can control deceleration in either forward or downward directions by changing the angle of the downstroke. Air speed of the bird is reduced, so the resultant relative wind striking the bird's wing, particularly the tip, is largely dependent on the direction of the wingbeat.

Aerodynamics of Flapping in Level Flight

Flapping can provide lift. An adult female condor with a full crop and an adult male with an empty one flew over Playa Chucho together; they both maintained the same speed and altitude, but the female flapped, and the male did not. In another instance, four adult males crossed the beach together maintaining the same altitude and air speed. One bird had a full crop and flapped, and the others, all with empty crops, glided. A full crop increases the weight-loading ratio for the wings by a factor of nearly 10 percent and should act to accelerate forward and sinking air speeds. Flapping apparently offsets these increases. A flapping adult male that I filmed canted to the right when I startled him. In two subsequent wingbeats, the top of left wing moved through a smaller arc than the right wing. The bird canted to the left and, in the third wingbeat, the left wing moved through a larger arc than the right. The differences in wingbeat movement seemed to level the condor.

Variation in lift between wings seemed directly related to the degree of wing movement. On the three different occasions I observed condors flap while circling, the bouts were apparent attempts to reduce sinking speed below the rate of ascent of the ambient air mass. Increased forward air speed would require the bird to exert a greater centripetal force to maintain a circular path with the same radius, and this in turn would increase sinking speed. Flapping, then, seems important to a circling bird because of its capacity to reduce sinking speed without increasing forward air speed.

Relationships between forward air speed and flapping rate for 42 condors and 5 turkey vultures crossing Playa Chucho were not statistically significant (r=+0.14 and 00.03, respectively). Other instances where flight speed seemed to be independent of wingbeat frequency were reported by Greenwewalt (1960) for a ruby-throated hummingbird and Tucker (1966) for a budgerigar. I did find, however, a significant correlation between the flapping rate of the condors and turkey vultures and their sinking speeds (Figures 38 and 39).

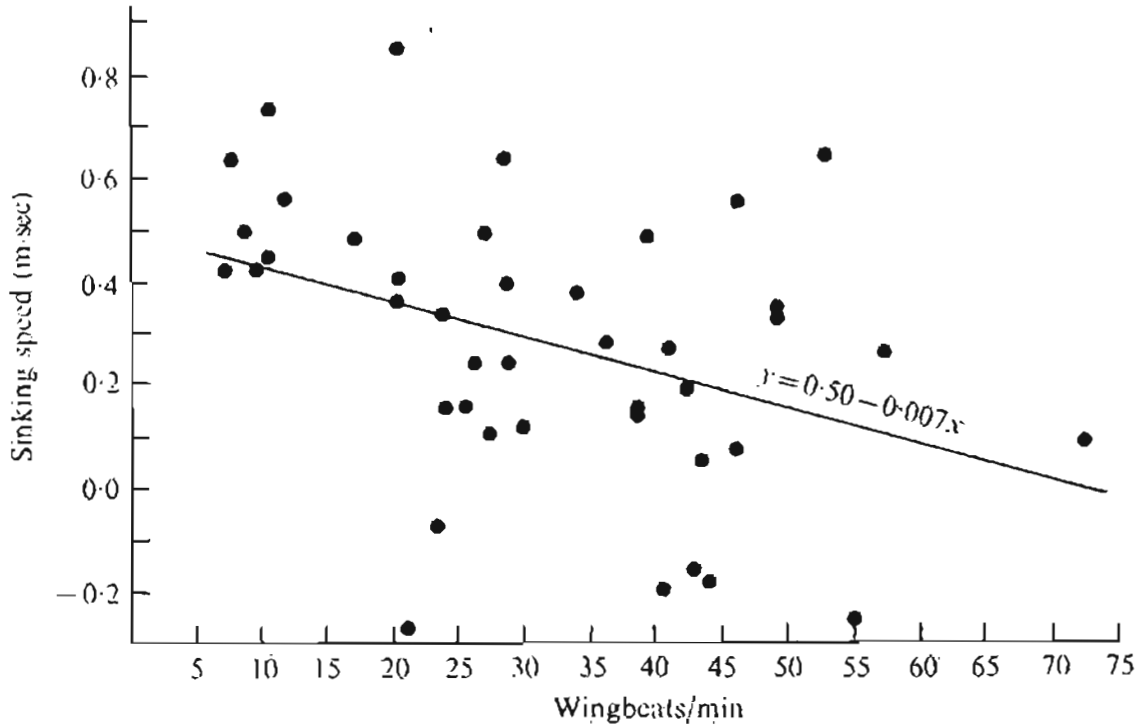


Figure 38. Sinking speed related to flapping rate for 42 condors (r=-0.40, p<0.05).

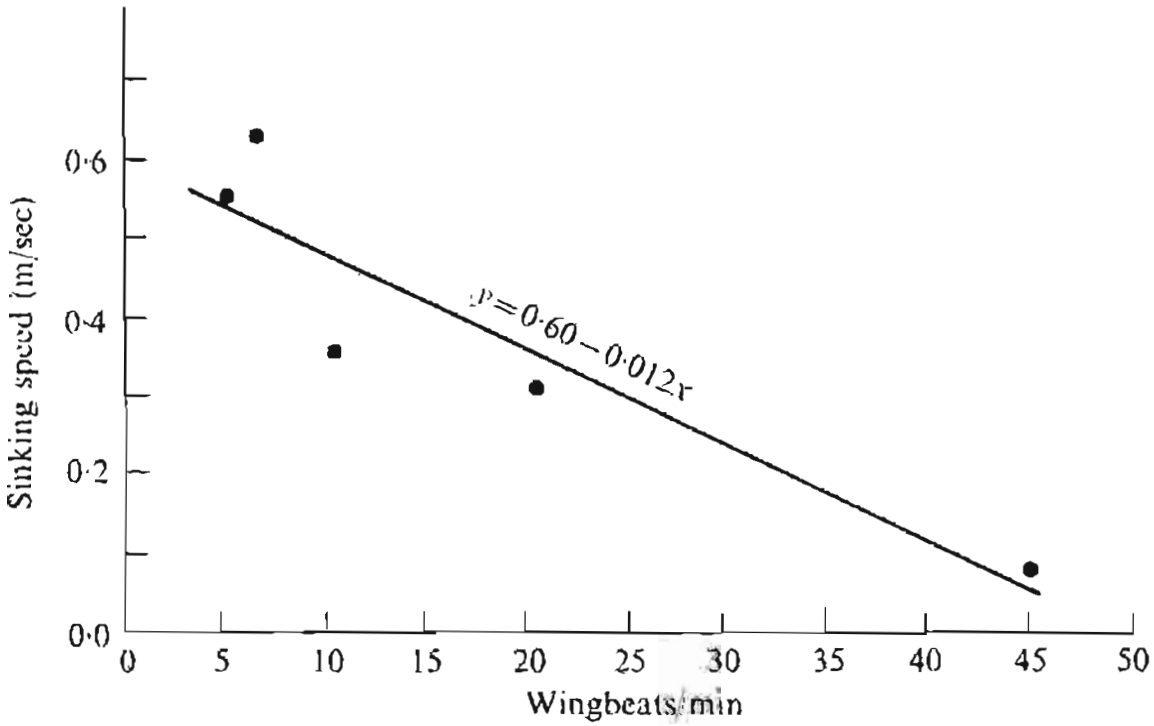


Figure 39. Sinking speed related to flapping rate for five turkey vultures (r=-0.92, p<0.05).

Vector Estimates For Relative Wind in a Wingbeat

To determine how flapping might act to produce lift forces I analyzed a wingbeat cycle in detail by using qualitative data from the cine film and quantitative data recorded on Playa Chucho. I used film to trace the path of movement made by the tip and midwing sections from a side view, so that I could obtain approximations of the relative wind direction for different parts of the wingbeat cycle (Figure 40). In still air, the wing in a downstroke would probably encounter a relative wind at an angle of attack larger than the stalling angle. However, if the condor is moving forward, the resultant relative wind would strike the wing at a smaller angle of attack. In the film, I found no instances of feather flutter on the dorsal wing surfaces of condors in level flapping flight, an indication that the boundary layer remained attached.

I obtained a rough assessment of the resultant wind velocity striking the flapping wing in normal flight by combining vector quantities for the relative wind encountered by the body with estimates for supplementary air movement produced by wing motion. For an estimate of the relative wind, I used a value of 14 m/sec striking the body from an angle of 4^{o} below the horizontal, the mean air speed monitored for 42 flapping condors crossing Playa Chucho at a glide angle corrected for equilibrium gliding in still air. I computed estimates for midwing and tip velocities for a flapping wing in still air with data from an adult female condor.

I estimated the approximate distance traveled by the wingtip in the downstroke as the length of the arc traversed by the wing in a circle with a diameter of 2.77 m, the approximate span of an adult female. The wingtip moves through an angle of approximately 90^{o} in the downstroke (Figure 37c, e). I calculated the speed of the tip moving through the air by dividing an estimated value for the distance traveled by a value for the downstroke duration. An adult female in level flight flapped at a mean rate of 1.8 cycles/sec; in the film analysis, I estimated the downstroke duration as 61 percent of the wingbeat period (Table 73). Hence, an estimate of the

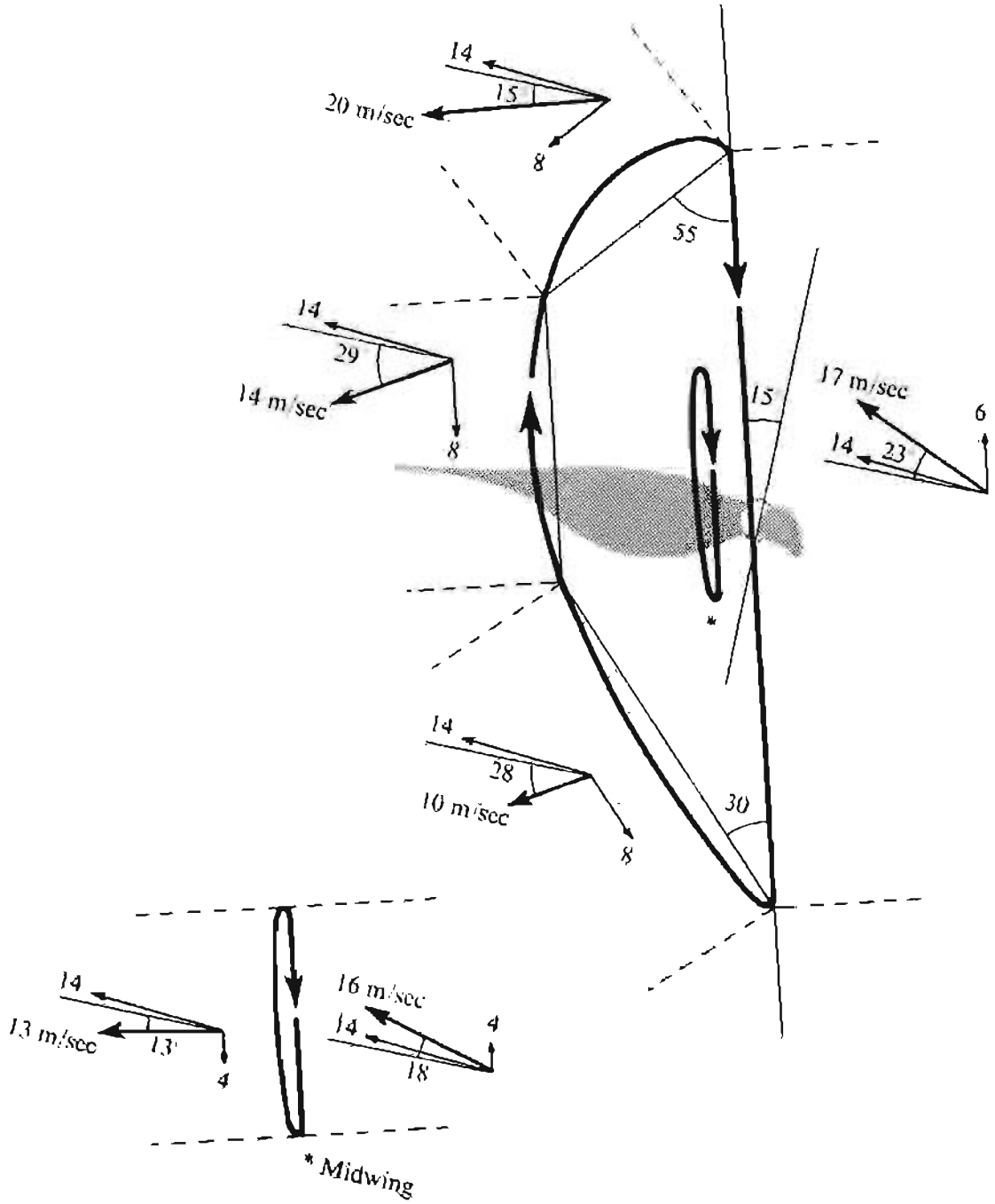


Figure 40. Wingbeat path at the tip and midwing section with vector estimates for relative wind velocity in four arbitrarily defined phases of the cycle.

average speed of the wingtip during the downstroke was calculated as

$\pi(2.77 \text{ m})(90_o/360_o)(1/1.8 \text{ sec})(0.61) = 6 \text{ m/sec}$

For the upstroke calculations I adjusted the value for the diameter from 2.77 m to 2.33 m to secure an estimate of the arc length traversed by the tip of a wing flexed to the degree shown in Figure 35d. Taking the upstroke duration to be 39 percent of the wingbeat period, I derived an estimate of 8 m/sec for average wingtip speed in the upstroke relative to the body. Air speed values relative to the body of 4 m/sec for both downstroke and upstroke were calculated for the midwing area with estimates of wing movement across an arc of 75^o for a circle with a radius of half the wing span. I estimated the duration of the upstroke at midwing as 43 percent of the wingbeat period and the downstroke as 46 percent (Table 73).

To obtain estimates for the resultant wind velocity striking the wing during different phases of the cycle I first simplified the diagram of wing tip movement by reducing it to a trapezoidal configuration (Figure 40). Then I computed the resultant wind vector for each of the four sides or phases of the stroke. The sides of the trapezoid approximate to the direction of movement, and the values for air speed produced by the wingbeat are only averages; the computations are, at best, rough and average estimates describing complex and rapidly changing conditions. They are valuable, however, for comparing large-scale differences and for illustrating how a wingbeat may act to provide lift.

The lift generated by an airfoil is directly related to the square of the air velocity passing over it. Thus, in the downstroke, the change in air speed of 14 m/sec to 17 m/sec at the tip, and increase in air speed of less than 25 percent, would act to increase the lift force by almost 50 percent when other conditions remained constant. It is unlikely that this substantial increase in offset by a reduction in lift during the upstroke. At the tip, for example, an air speed of 20 m/sec at the top of the upstroke compensates for the reduction of 10 m/sec at the beginning so that, in

general, gliding air speed is approximated by the average resultant air speed during the upstroke, whereas it is exceeded during the downstroke. The duration of the downstroke is longer than that of the upstroke, so an increase in air speed across the tip predominates during the wingbeat period.

Angles of Attack in a Wingbeat

As the wing moves, conditions other than air speed change to affect the lift force provided; the angle of attack of the airfoil is a critical variable. To provide optimum lift forces, the flapping wing must rotate or twist to accommodate the changing angle of the resultant relative wind, especially at the tip where these changes are greatest. Vector differences in Figure 40 suggest that the wingtip angle of incidence should tend toward the negative during the downstroke, when the relative wind is directed upward more steeply. In the upstroke, when the relative wind moves downward, the angle of incidence providing the greatest lift must be positive. I examined the film and found that the wing posture conforms to this model (Figure 37a-g). In the downstroke (Figure 37a), most of the wing has a negative angle of incidence, and the angle increases toward the tip. For the upstroke (Figure 37d), the angle is positive, and, here as well, the effect is more pronounced distally.

At the tip, each primary may act as a separate airfoil that affects and is affected by highly complex airflow conditions characteristic of wings with slotted tips. To secure more information on the relation of angle changes for wind and wing, I used estimates for the midwing area, where the pattern of airflow is simpler, even though wingbeat effects are reduced. Vector quantities describing resultant wind for the midwing are shown in the inset of Figure 40. I obtained an estimate for the angle of incidence during an upstroke phase by measuring certain features of the image projected from the frame of cine film used to trace Figure 37d. Using a ratio of image wing span to an estimate of the actual span, I secured a scale for computing an estimate of 13 cm

for the width of the projected midwing area. Into this value, I divided 35 cm, an estimate of the length of the wing chord, to obtain an approximation for the sine of the angle necessary to project the surface area observed. Because the long axis of the bird and the flight path were directed straight away from the camera, the full 22^{o} angle computed should represent the angle of incidence. If the relative wind strikes the bird from an angle of 13^{o} above the horizon, as computed and illustrated in Figure 40, the angle of attack would be the difference; that is, 9^{o}. If the secondaries bent upward on the trailing edge in passive response to the pressure forces, the angle would approach zero and lift forces would diminish. Instead, the wing apparently remains rigid and in doing so maintains an angle of attack that should produce a substantial lift force. For an airfoil with an aspect ratio and profile like that of the condor wing, an angle of 9^{o} is within the range of angles of attack most effective, *i.e.* those associated with maximum glide ratios for a wide range of air speeds.

The wingtip path described for a condor wingbeat resembles that noted for other birds (Storer, 1948; Cone, 1968); the forward orientation of the downstroke is not peculiar to condors. If this axis were directed posteriorly 15^{o} from the vertical instead of anteriorly, as shown in Figure 40, the high air speeds attained in the downstroke would occur in the upstroke instead, and relatively reduced air speeds would characterize the downstroke. Mechanical efficiency for the lever system of the downstroke is much greater than that of the upstroke because the muscles are ventral to the wings. Thus, the downstroke is the optimum stage of the wingbeat cycle for producing and withstanding maximum lift forces—the forces incurred with increased air speed over the surface area of fully extended wings.

Flapping and Propulsion

In each of four different aerial chases when a pursued condor flapped more than the pursuer, the distance between them increased in the horizontal but not in the vertical plane. The

wingbeat pattern may have been different from that discussed previously, or perhaps the bird flew faster with wings somewhat flexed while compensating for increased inking speed by flapping. In another situation, an alarmed female took off, flapping 53 times, to travel an air distance of 227 m horizontally and 14 m vertically (Table 74). In take off, the relative wind velocity is less than in gliding flight, and average resultant lift forces act in different directions. The wing encounters the wind at such steep angles of attack that the lift-drag ratios must be much less than those of level flight; even so, the resultant force has a positive thrust component directed toward the flight path during both upstroke and downstroke (Figure 41). In the diagrams of Figure 41, it can be seen that forces of an upstroke in level flapping flight produce a small component opposing forward motion. Although the lift/drag ratios are stylized in this diagram, the effect would also be present with actual ratios that are larger and explains why condors flapping across Playa Chucho maintained significantly lower air speeds than those that glided.[3]

Although diagrams in Figures 40 and 41 may describe general conditions for the major wing area, the complex airflow pattern around the primaries probably produce wingtip forces with quite different vectors. Dissimilarities in individual wingbeat action also were not considered in this analysis. I noted substantial differences in rates of descent by flapping birds that seemed independent of air conditions. For the 42 flapping condors observed crossing Playa Chucho, the mean difference in descent distance according to the presence of flapping was 0.42 m per wingbeat (0.007 m/sec for each wingbeat per minute, Figure 38), compared to values of 0.9 and 1.4 m obtained in two separate observations of flying pairs. In the first pair, A flapped three times; B did not flap and descended 2.7 m more than A. In the second pair, A flapped 42 times; B did not flap and descended 60 m more than A. These differences in descent distance related to flapping are probably due to variations in wingbeat movement tuned to unique flight

Table 74. Summary of data recorded on the flapping escape flight of a subadult female condor. Ground measurements are corrected for a 2 m/sec horizontal wind that blew perpendicular to the flight path.

Horizontal air distance traveled	227 m
Vertical distance traveled	14 m
Angle of powered climb	3°30'
Number of wingbeats	53
Flight duration	21.2 sec
Average air speed	11m/sec
Average speed of ascent	0.7 m/sec
Average vertical distance traveled per wingbeat	0.3m
Minimum power output per kg muscle necessary for ascent (disregarding power required for level flight)	21 W
Mimimum power output per kg muscle	54 W

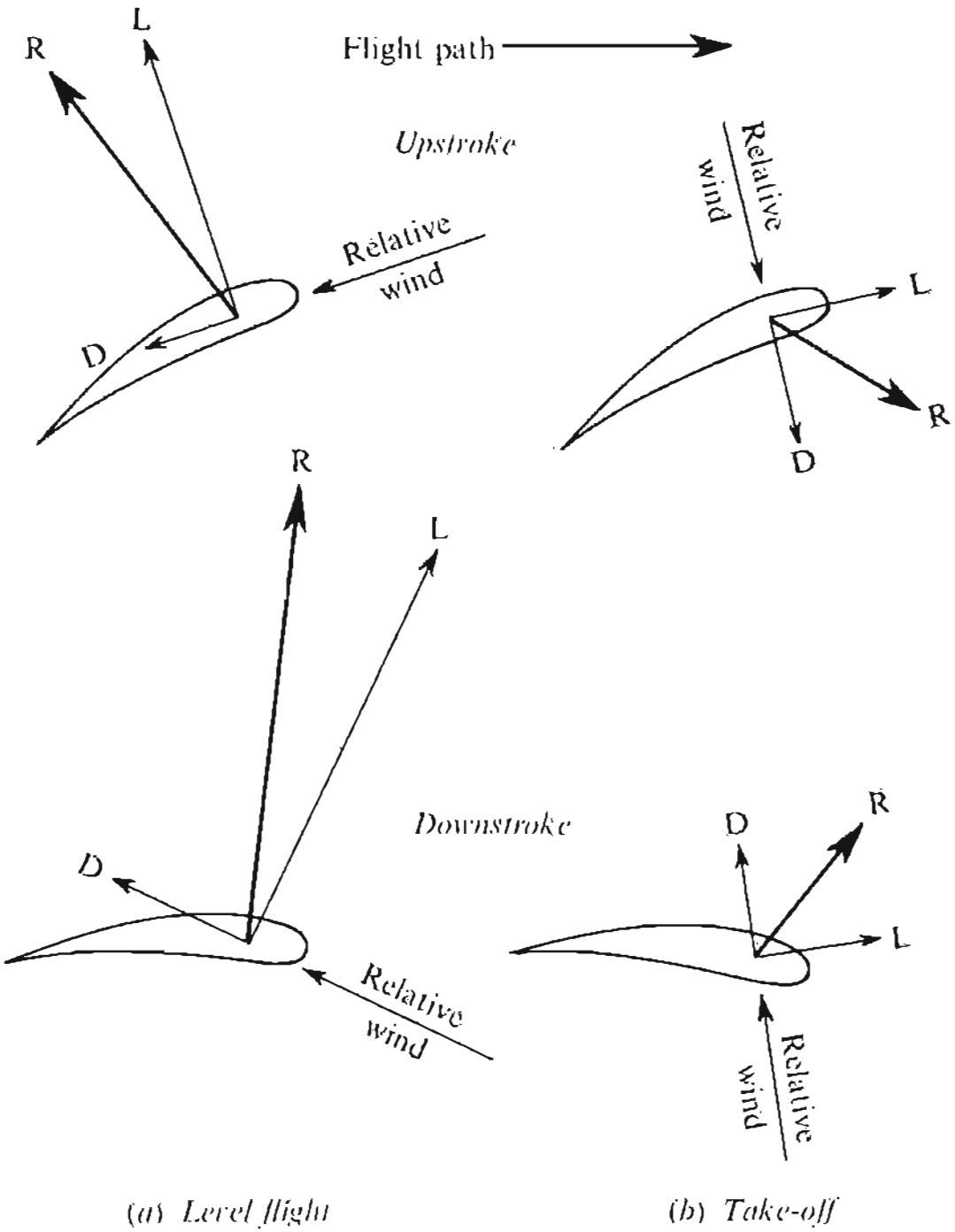


Figure 41. Approximate directions for the resultant forces produced by airfoils under conditions simulating flapping flight.

conditions.

Power in Flapping Flight

An estimate of the minimum power necessary to sustain a bird in level flight can be computed with the equation

$$P=mgV_s, \quad (10)$$

where m is the mass of the bird, g is acceleration due to gravity, and V_s is the sinking speed for equilibrium gliding in still air. Power output in watts (W) can be described as the ratio of power necessary for level flight to the body or muscle mass of the bird. Estimates of minimum power output per unit mass of wing muscle were computed using the equation

$$P/m=gV_s/z, \quad (11)$$

where z is the percent of body mass represented by wing musculature. According to Fisher (1946), z is around 33 percent for the Andean condor and 52 percent for the turkey vulture. I used adjusted mean values of V_s (Table 75) to secure estimates of 33 w/kg wing muscle for the condor and 17 for the turkey vulture as the minimum power output necessary for sustained flight in still air.

In addition to these estimates of power required for flight, I secured one measure of the power generated by recording certain features of an escape flight by a startled condor (Table 74). This condor, a female, fed on a beach below a long ridge. Simultaneously, two assistants and I flushed her from different points so that her only escape route was over the ridge. She flew toward the ridge flapping steadily in the longest uninterrupted series of flaps that I ever recorded for a condor. Apparently unable to fly over the ridge, she alighted near the top and ran to the crest. The maximum power output possible was probably approached in this exceptional effort. Considering both the power necessary for level flight and that expended in the ascent, the wing

Table 75. Estimates for the rate of flapping required to maintain level flight.

	Condor	Turkey vulture
Average sinking speed for equilibrium gliding in still air (V_v)--corrected data[a]		
Gliding birds	1.2 m/sec (n=15)	--
Flapping birds-extrapolated to a flapping rate of zero	1.0 m/sec (n=42)	0.9 m/sec (n=5)
Weighted average	1.1 m/sec	0.9 m/sec
Regression coefficient (b) for x = flapping rate and y = sinking speed (Figs. 38, 39)	-0.007	-0.012
Flapping rate necessary to maintain level flight ($-V_s/b$)	160 wingbeats/min	75 wingbeats/min

[a] Each sinking speed value adjusted by adding an estimate of the vertical wind component that would satisfy a discrepancy noted in estimates of drag (Table 71).

muscles of this female condor produced a minimum of 54 w/kg muscle. The output estimate for this brief and exceptional effort is about half that recorded for a pigeon in similar circumstances (Pennycuick and Parker, 1966).

To evaluate the relationship between estimates of the power output generated by the exceptional effort of this female and the output necessary for sustained flight, I examined similar data on human muscle. In a brief and maximum effort, human muscle can produce a power output of about 40 w/kg muscle (Dickinson, 1928; Parry, 1949), whereas the maximum sustained output has been calculated at about 17 w/kg muscle (Henderson and Haggard, 1925; Parry, 1949). If this output ratio for exceptional and sustained efforts (40:17) is similar for condor muscle, about 23 w/kg muscle are available for sustained flight, if we assume that the mechanical efficiency of the flight systems for exceptional and sustained efforts are similar. Apparently then, less than the minimum requirement of 33 w/kg muscle necessary for level flight are present; oxygen would not be supplied fast enough to maintain the necessary power output. Behavior data support the hypothesis that the condor is incapable of sustained level flight in still air; in situations where the air seemed still, I never saw a condor fly for an extended period without losing altitude rapidly (see also pp 60-62). Pennycuick (1969), in an analysis of power output per unit weight of birds, cited observations of flight by bustards and African vultures that support his estimate of 12 kg as the upper limit for the weight of birds able to fly horizontally at all. The weight of an adult male condor approximates that point.

Comparison of Condor With Turkey Vulture

I obtained no comparable data for maximum outputs in exceptional efforts by turkey vultures, so I could not obtain similar estimates for this smaller bird. Three other comparisons, however, indicate that the turkey vulture probably can maintain level flight in still air for longer periods than the condor: (1) The estimates for the minimum power output/kg wing muscle

necessary to sustain level flight are greater for the condor than for the turkey vulture (33:17) largely because a greater proportion of the turkey vulture mass is composed of wing muscle. (2) The average mass of turkey vulture per unit of projected wing area is about half that of the condor (Table 68). This twofold difference in weight loading is significant in considering the effect of flapping on sinking speed; assuming similar conditions for both flapping systems, the condor must flap at a greater rate than the turkey vulture to obtain the same effect. (3) Some evidence for this difference in flapping efficiency is presented in the regression analyses of sinking speed and flapping rate. Changes in the flapping rate appeared to affect the sinking speed of the turkey vulture more than that of the condor (Figures 38 and 39). By dividing the regression coefficient for flapping rate and sinking speed into estimates of the average sinking speed, I obtained values of 160 wingbeats/min for the condor and 75/min for the turkey vulture as rough estimates of the rates necessary to maintain level flight (Table 75). The data in this comparison are in good agreement with expectations projected from the weight loading comparison; but they can only serve as possible indications, because the difference between the two regression coefficients is not statistically significant.

In sum, on the basis of flight performance and physical dimensions, the turkey vulture appears capable of more extended flights in still air than the condor. Whether or not the smaller vulture can maintain level flight for extended periods in still air depends, of course, on the maximum level of sustained power output by the muscles and the efficiency of the flapping system.

FLIGHT MANEUVERS

Circling

The circling flight pattern allows a condor to ascend in a volume of rising air of limited size. Typically, both wings are completely extended and the tail fully expanded. During one 10 min period when a condor circled 50 to 100 m away from me at eye level, I watched closely for feather movement to obtain information on the control and maintenance of the circling pattern and the condition of the boundary layer of air around the bird. I saw only the primaries and the tail move in apparent steering maneuvers. Both wings remained fully extended at all times during the observation. The secondaries did not appear to move and maintained a constant angle of incidence. Wing and tail coverts and body feathers did not flutter at any time which indicated that the boundary layer of air remained attached in those areas.

Method of Study

With the aid of two assistants I was able to secure estimates for forward speed, banking angle, and radius of each circle by two adult males in air with little or no extensive horizontal movement. We stood on a nearby ridge while two birds circled 90 to 180 m above a canyon floor, at a position about eye level with us. I used a level sighting scale to estimate the radius of each of 11 circles in wingspan units. This was done by mounting a level ruler on a swivel-head tripod and sighting over it from a fixed distance set by a 30 cm length of aluminum tubing. When the circling bird was sighted over the ruler, either coming directly toward or directly away from us, I measured the width of the wingspan in millimeters and noted at what point on the ruler the condor was sighted. Then, keeping the sighting device fixed, I waited until one half of the circle was completed and recorded that point on the ruler over which the bird was sighted. Thus, with three values, I was able, first, to translate millimeters to wingspan units and then obtain an estimate of circle's diameter in wingspan units. In these observations, the circling patterns seemed unusually stable, with no noticeable lateral or vertical deformations in the path, so I considered the distance traveled as the perimeter of a circle with the observed diameter, $\pi d/2$,

with *d* as the diameter of the circle in meters. In converting wingspan units to meters, I used the mean wingspan values listed in Table 68, calculating each according to the sex of the circling bird. One assistant recorded durations of individual circle patterns, the other, banking angles. By sighting over a drawing compass that had one leg clamped horizontally, the assistant estimated the angle of bank when the bird circled directly toward or away from us,. A paper tracing of the compass position recorded the angle. Later, using a protractor on the tracing, I expressed the estimated angle of banking in degrees.

Dividing the estimated air distance in each circle by the duration, I obtained a mean and standard error of 6.4 ± 0.04 m/sec for forward air speed on circular paths, with a mean radius of 16 m. Assuming that conditions of equilibrium flight existed in a volume of air that was not rotating, I computed estimates for the expected banking angle φ_e with the equation

$$\tan \varphi_e=(V_f)^2/rg, \qquad (12)$$

where V_f is forward air speed and *r* is the circle radius. For the 11 recorded instances of circling, I obtained a mean value of 15^o (95 percent confidence intervals: 13^o, 18^o), compared to the observed mean of 16^o (95 percent confidence intervals: 12^o, 20^o). The similarity provides evidence that values for forward air speed and circle radius were reasonable estimates.

Sinking Speed and Glide Angle

Resultant air speed of circling condors combined forward air speed, which can be observed and measured as described above, and sinking air speed, which cannot be observed and measured if the bird circles in an air mass moving vertically at an unknown rate. With equation 5, I calculated estimates for lift coefficient and descent rate using mean and confidence interval values for observed forward air speed. Assuming air density (p) as 1.17 kg/m^3, forward air speed as 6.4 m/sec, and sinking air speed as zero, I obtained a lift coefficient C_L=4.4, a value exceeding

any likely maximum. The resultant air speed must be greater, augmented by a sinking air speed. To secure estimates of sinking air speed, I used lift coefficient values of C_L=1.0 and C_L=2.0 to calculate approximations of the resultant air speed. Then, with 95 percent confidence interval values for observed forward air speed, I obtained minimum and maximum estimates for sinking speed and the glide angle in a vector analysis (Table 76). So, according to these computations, for example, a condor circling with a forward air speed of 7.2 m/sec and a lift coefficient of C_L=2.0 will lose altitude unless he is flying in an air mass that ascends at a rate equal to or greater than 6.2 m/sec. Estimates for sinking speed, and rate of ascent by the air, derived in this manner ranged from 6 to 12 m/sec.

These estimates also exceed any likely maximum. According to Pennycuick (1953), dry weather thermals in Africa have typical rates of climb of 2-4 m/sec. Although a glider can attain a rate of climb of 5 m/sec in a strong dust devil, the area of lift is usually turbulent and narrow in scale (Pennycuick, 1972). The condors we observed did not appear to encounter any turbulence at all. Possibly, these birds were circling in moderate dust devils, where rotating air moved in a direction opposite to that of the condors, which would permit them to obtain significantly higher air speeds than their ground speed revealed. Because the banking angle is a response to the inertial tendency, ground speed and not air speed is the determinant. Hence, the close agreement we found between observed angles and those generated on circle size and ground speed could be obtained with a wide range of air speeds, allowing the possibility that these birds did circle "upwind" in columns of rotating air. Such an orientation would permit more rapid ascent because, for a given air speed, relatively less energy would be needed to counteract centrifugal force.

I found no tendency for condors to circle either to the right or to the left more frequently. Pairs often circled at the same level so that each bird moved in a direction opposite from the

Table 76. Extimates of sinking air speed and glide angle for circling condors.

Assumed lift coefficient (C^L)	Computed resultant air speed - m/sec (Derived from C_L value with equation 5)	Observed forward air speed (6.4m/sec) 0 95 confidence intervals	Estimates for: Sinking speed (m/sec)	Glide angle
1.0	13.4	5.6	12.2	65°
1.0	13.4	7.2	11.3	58°
2.0	9.5	5.6	7.7	54°
2.0	9.5	7.2	6.2	41°

other. I saw a group of about 40 black vultures in Colombia circling together and in the same direction. This coordination may have been a social response, or perhaps the birds flew in such a rotating thermal. In East Africa, Pennycuick (1972 and pers. comm.) noted coordinated circling patterns by flocks of white pelicans and flocks of European cranes, where all circled in the same direction; they did change direction from time to time but did so as a unit.

Two important constraints can affect minimum sinking speeds attainable while circling: (1) In general, sinking speed increases as the radius of the circular flight path decreases. When flying in a straight path, an increase in the forward air speed up to an optimum level would reduce sinking speed; but in the circling pattern, any increase results in an energy loss necessary to offset centrifugal forces. I saw a circling adult female suddenly descend 200 m in a spiral descent, characterized by radii of diminishing size for each circle and by steeper banking angles. Reduced radii and higher air speed will increase the centrifugal force markedly; banking at a steep angle provides a component of lift force to counteract that force. The rate of descent is regulated according to the magnitude of the lift component acting vertically in opposition to gravity. (2) Another important condition regulating sinking speed is the angle of attack of the wing. Steep descents may act to increase the angle of attack above the stalling angle. The lift coefficient drops rapidly when the boundary layer detaches. As can be seen in Table 76, the estimates for glide angle are so large that a relative wind will strike the wings at an angle of attack well above the stalling angle for most airfoils.

The slotted wingtip of the condor is particularly suited to these constraints. A multi-slotted airfoil can produce lift coefficients up to C_L= 2.3 and at very high angles of attack (Prandtl and Tietjens, 1934). The primaries at the tip of a fully extended wing are in the configuration of a multi-slotted wing and probably produce substantial lift forces on a steep glide angle into a reduced relative wind.

Inferences on Air Movement

I estimated the rate of ascent relative to the ground for circling condors at different stages of the flight to obtain data describing possible changes in flight and air movement at different altitudes (Table 77). In all but one of six sequential observations, the rate of ascent increased as the bird gained altitude; this suggests that changes in air movement enhanced flight conditions. If the lateral dimensions of the ascending mass of air expanded, the bird could increase its air speed without changing the banking angle. Such increases up to the optimum would reduce sinking speed in equilibrium flight conditions, as shown in the estimates of Table 76. For example, assuming the rate of vertical movement by the air and the lift coefficient for the condor's wings remained constant at C_L=2.0, an increase of 1.6 m/sec in forward speed would provide an increase in the ascent rate of the bird relative to the ground by 1.5 m/sec.

Changes in the rate of ascent by the condors could mirror changes in the rate of vertical movement by the air. Cone (1963), in his discussion of the thermal shell, a bubble of air with internal circulation around a vortex ring core, stated that the ascent rate of the thermal should decrease at higher altitudes. This model is of marginal value, however, in considering vertical air movement in the steep relief of the Colombia habitat. Here, ascending air is undoubtedly affected by a complex combination of local thermal conditions, general mountain-and-valley breezes, and particular orographic characteristics producing local declivity currents. Condors probably use ascending currents at particular sites where different wind sources and modifiers act together optimally to amplify the ascent rate of air. In one such location, I saw a condor ascend about 1000 m in a single bout of circling.

I found no significant differences in durations of individual circle flight patterns between male and female condors, but I did find a difference in durations recorded from two different areas. In the Cerro Illescas, the strong south wind characteristic of most of the coast is

Table 77. Differences in the ascent rate of circling condors at various altitudes above the ground in the Colombia study area.

Sequence no. for timing	Altitude above ground at timing (m)		Time interval (sec)	Mean rate of ascent (m/sec)	Within sequence differences for:	
	Begin	End			Altitude at start of timing (m)	Mean rate of ascent (m/sec)
1	30	120	40	2.2		
2	120	300	40	4.5	+90	+2.3
1	45	120	120	0.6		
2	120	460	120	2.8	+75	+2.2
1	245	265	28	0.7		
2	305	315	13	0.8	+60	+0.1
3	395	405	14	0.7	+90	-0.1
4	580	598	12	1.5	+185	+0.8
1	25	115	180	0.5		
2	120	640	120	4.3	+95	+3.8

substantially reduced; vertical currents seem produced primarily by local thermal conditions. In this area. the duration of individual circle patterns was generally shorter than those of condors observed circling in the Paracas area. In the Cerro Illescas, 47 of 67 circling durations recorded were less than 17 seconds long, whereas none of five recorded in Paracas was this brief, a significant difference.[4] Cliff-deflected winds in Paracas produce updrafts that seem to be more turbulent and less extensive vertically, but more so laterally, than those produced in thermal systems. These contrasts contribute, no doubt, to the overall conditions responsible for longer durations, as well as to the dearth of circling patterns seen in Paracas. Although total observation time in Paracas was greater than in the Cerro Illescas, the difference in the observed frequency of circling flight was no less marked than that represented by the sample sizes of the circling durations noted above.

Differences in durations of circle patterns for condors in the Cerro Illescas and in the Colombia study area were insignificant, but within each sample I found a significant positive correlation for duration and altitude above the ground (Figures 42 and 43). For the Peruvian data, the regression coefficient described an increase of 0.5 sec/100 m above the ground, whereas records from the Colombian area provided a coefficient of 5 sec/100 m. These coefficients differed significantly.[5] Apparently, circling condors in ascent either decrease forward air speed, increase the circumference of the circular path they follow, or both. Moving air masses probably increase in size as they ascend, and the longer durations may reflect an increase in the distance traveled. If longer durations may reflect an increase in the distance traveled. If so, the condor can fly faster at a given banking angle to approach more optimum glide angles. If the optimum angle is attained and forward air speed becomes constant, further increases in circle size would produce longer circle durations. Possibly, condors do not attempt to ascend above a certain rate or a certain point and regulate their ascent by controlling air speeds; in this scenario, they would

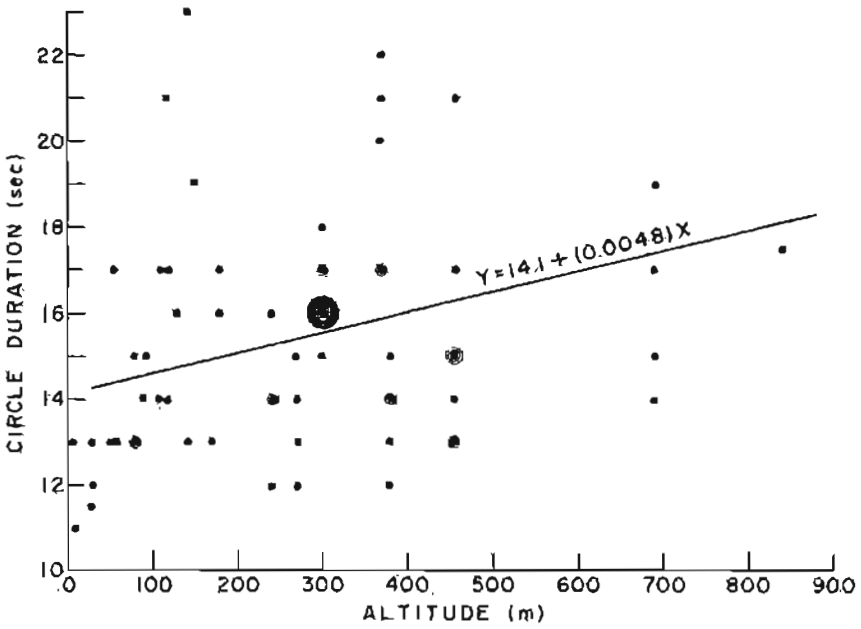


Figure 42. Duration of individual circle patterns and altitude above the ground by soaring condors in the Cerro Ilescas (n=67, r=+0.34, p<0.01).

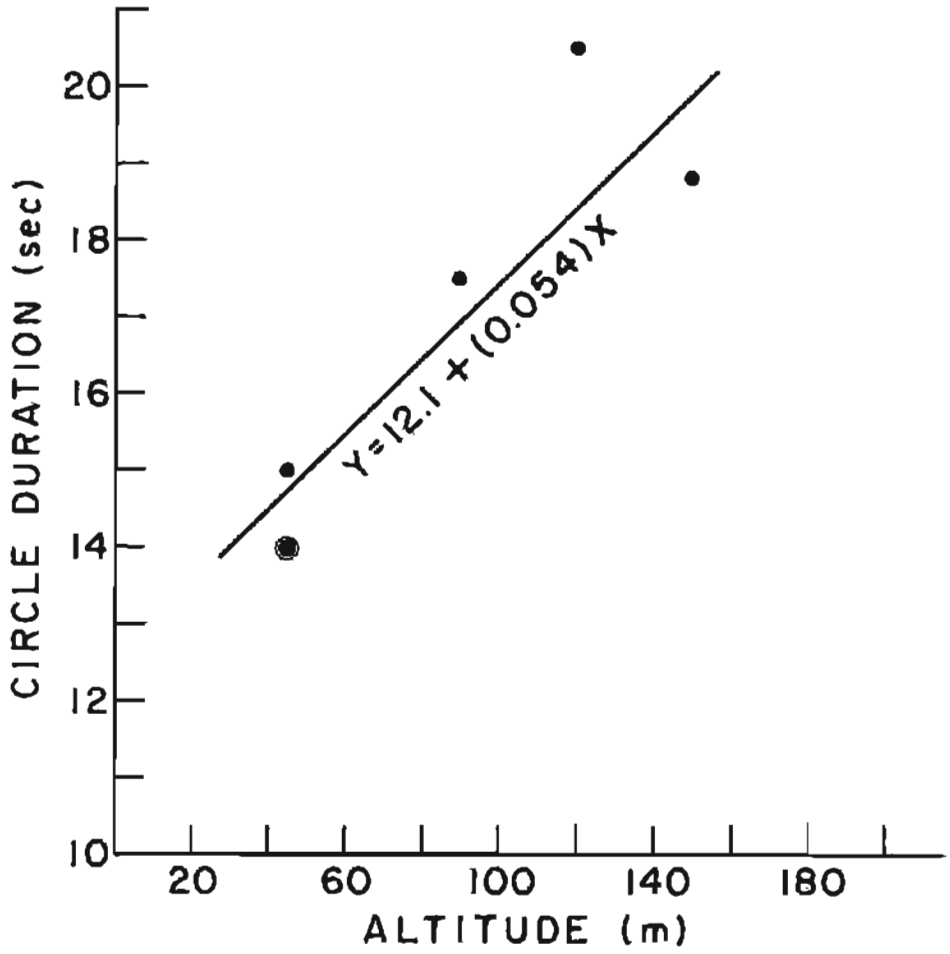


Figure 43, Duration of individual circle patterns and altitude above the ground by soaring condors in the Colombia study area (n=6, r=+0.91, p<0.05).

glide more slowly at higher altitudes. In either case, the difference in regression coefficients suggests that ascending air masses increase either in size or rate of ascent more rapidly in the Colombia study area than in the Cerro Illescas of Peru. Such differences may well exist, because climatic conditions and relief of the country in the two area vary so greatly.

Other Factors

Condors that turned their heads, as though examining something below them, often circled more slowly. In Colombia, I timed circle durations of 17, 18 and 23 seconds by an adult male watching me closely; all durations exceeded the mean of 15.5 seconds (standard error, 0.3) for 73 durations recorded in Colombia and the Cerro Illescas. I recorded the longest duration, 29 seconds, when an adult male watched and finally landed near a sleeping calf.

We rarely observed flapping during circling flight. Calculations for estimates of reduced sinking speed by flapping while circling suggest that, for observed flapping rates, sinking speed is only marginally affected (Table 78); for the highest observed flapping rate (23 wingbeats per minute), the relation in sinking speed was calculated to be more than 0.16 m/sec, only about 15 percent of the estimated sinking speed for level flight in still air (Table 75). Flapping, then, seems useful to a circling condor only in those instances where the difference between sinking speed of the bird and ascent rate of the air is sufficiently narrow, so that flapping can prevent altitude loss or perhaps provide a means of slow ascent to a higher altitude, where air conditions are more favorable.

Steering

Dipping One Wing

The steering movement most easily recognized in condor flight is a dipping motion of a single manus that involves the downward displacement of from one primary feather to the entire manus (Plate 28). Rotating from a positive to negative angle of incidence, the manus drops

Table 78. Estimates of a reduction in sinking speed due to flapping while circling.

Duration of circle pattern	No. wingbeats observed in each circle	Flapping rate-wingbeats/min	Calculated reduction in sinking speed-wingbeats/min x 0.007 (see Figure 38)
11	2	11	0.08 m/sec
13	5	23	0.16 m/sec
13	5	23	0.16 m/sec
13	3	15	0.08 m/sec

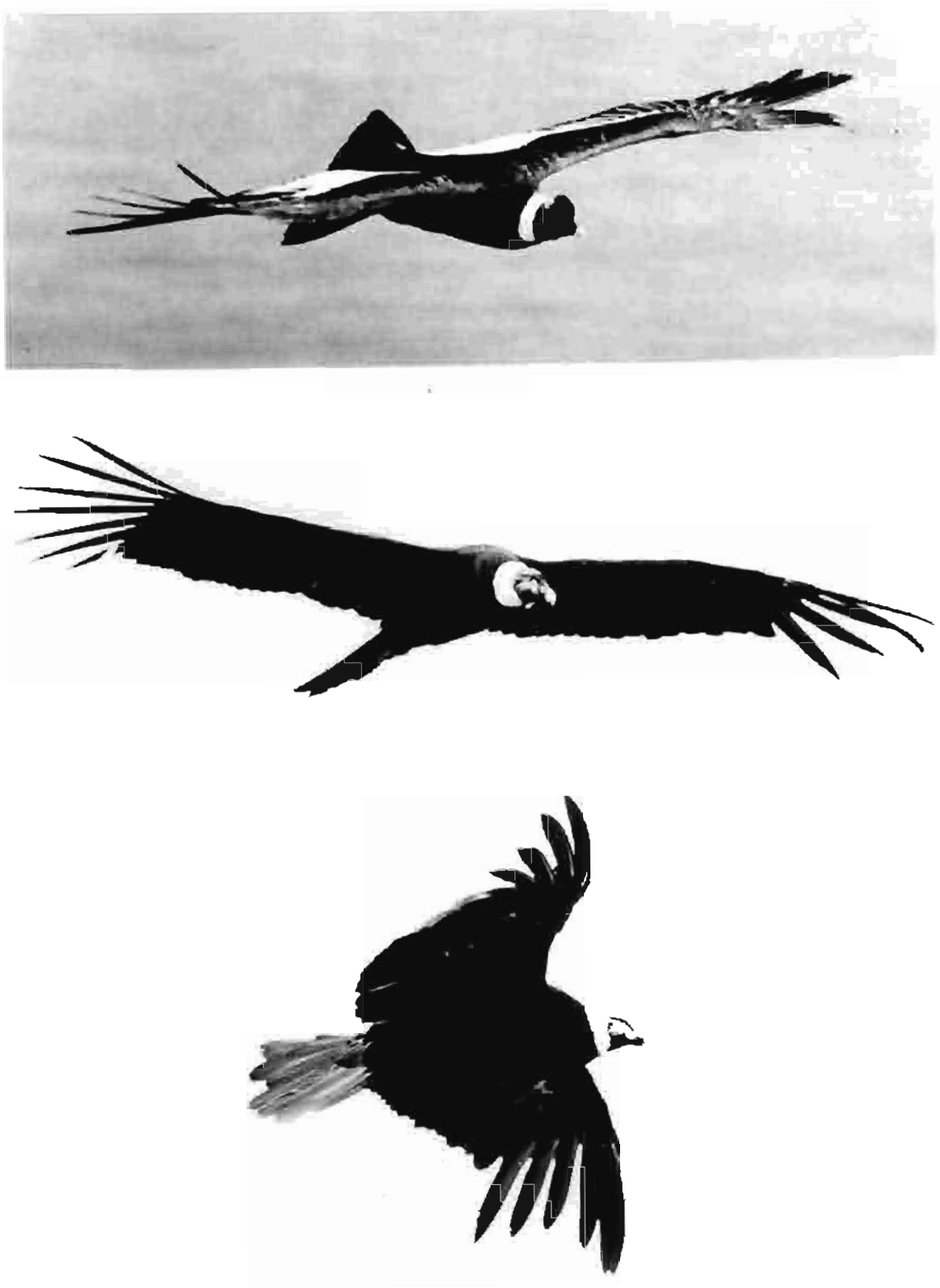


Plate 28. Condors in single-dip postures.

below the horizontal plane of the wings. In the depressed position, each primary feather bends downward more than the feather immediately posterior, and often beyond the degree of curvature typical of the primary feather at rest. Presumably the reduced lift of the dipped wing acts to turn the bird toward that side. From cine film of condor flight, I found that the degree of manus rotation, the number of primary feathers losing the upward curvature typical of gliding flight, and the severity of the turn all varied in a direct relationship. Gradual turns characteristic of circling flight succeeded dips where only the lead primary feather, moving only bout 15 cm at the tip, dropped to or slightly below the horizontal plane of the wings. Condors in pursuits or suddenly alarmed often dipped the whole wing; the long axis of the body dropped sharply down and toward the dipped wing, and the bird turned in a steep and accelerated descent. This turn often succeeded stalling situations.

Prior to landing, flex-gliding birds often alternated single dips from one wing to the other and descended in S-shaped flight paths. I could not detect individual movement by the primary feathers of flex-gliding condors when they single-dipped, but downward rotation of the full manus was evident. I saw an adult male, flex-gliding with lowered legs, advance his left leg before dipping the left wing. After recovering the wing, the leg moved back to the original position. When I yelled at a condor gliding by me, he dipped the outside wing and descended in a turn away from me. Frequently, condors canting to one side in turbulent winds leveled after single dipping the wing on the upper side. One condor followed this pattern with a double-dip pattern by dropping the other manus after leveling. A condor gliding round a coastal point of rocks single-dipped the manus nearest the cliff repeatedly. The bird tended to cant away from the cliff. After each dip, the bird gradually leveled; the dip pattern apparently counteracted stronger elements in the deflection current nearest the rocks. Immature birds often dipped one wing, paused, and then dipped the other. In general, immature condors seemed less stable in

flight than adults; the second dip may have regained trim or balance lost in the first motion.

Rotation of the Tail

Steering by dipping a single wing characterized flex-glides, rapid maneuvers, and flight in turbulent winds, whereas the tail appeared to control turn and circling flight in stable air. The direction of a coming turn could be predicted by noting the direction of lateral rotation by the tail. The elevated side of the tail indicated a turn toward that side, the turn following a pause after the tail moved. Koford (1953, p. 42) reported similar tail-steering maneuvers by the California condor. Apparently, the tail acts as an airfoil; by rotating the upper surface away from the direction of an intended turn, a lateral component of lift yaws the condor's posterior outward, and directs the anterior into the direction of the intended turn. I could detect no movement by the primary or secondary wing feathers nor any fluttering by the wing or tail coverts in response to tail movement by condors circling near me. Gyrating the tail up to 60^{o} from the horizontal, immature birds usually rotated the tail more than adults,. Adults rarely moved it across an arc larger than 30^{o}. Steering forces produced by the tail seem reduced and protracted in effect compared to those of the single dip, yet apparently they supplement those of the dip. In each of 18 photographs taken of condors in single-dip configurations, I found the tail was always rotated with the upper surface directed away from the dipped wing (Plate 29), presumably to act in concert with the wing to steer the bird. In seven of eight single-sips recorded on cine film, the tail moved before the wing.

Moving the Head

Occasionally, I saw flying condors turn in apparent response to head movement. As one condor glided over the observation beach, he watched me after turning his head to the left for several seconds. His body yawed in that direction. Then after turning his head to the other side for a similar duration, his body rotated back to a position parallel with the flight path. An adult

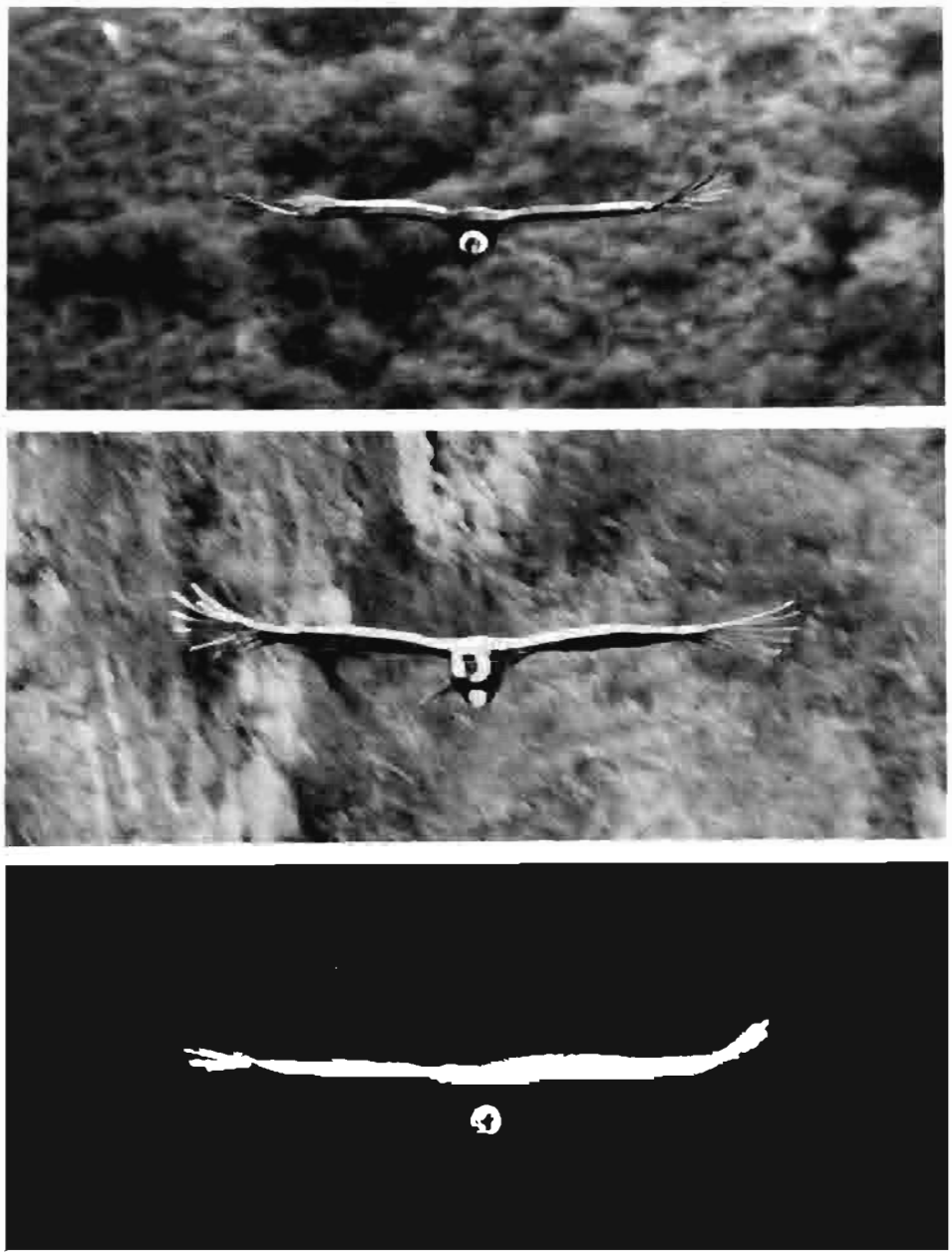


Plate 29. Variation in the angle of incidnece between right and left wings in gliding flight postures. Note the differences in projected width of the wing images.

male gliding in a declivity current at the edge of a cliff made little progress relative to the ground for several minutes. He turned his head from one side to the other five times and watched me standing behind. Each time he turned his head his body rotated through an arc of about 80^{o} in the same direction. I detected no tail or manus movements. A condor circling above me turned his head out away from the circular path regularly. Each time, ground speed was checked and the circular path distended as the long axis of the bird yawed to the outside momentarily. I saw an adult female gliding in straight flight hold her tail for an extended period in a position that usually preceded a turn to the right. At the same time, however, the head was rotated to the left. The steering forces of the two postures apparently canceled each other.

Other Methods

Infrequently, condors executed turns in other ways. One gliding condor flexed a wing slightly while preening feathers on its leading edge. The condor turned to that side, probably in response both to wing flexion and head movement. While landing, an immature male canted to one side; he flexed the elevated wing slightly and leveled immediately. Arching of a single wing may at times be used for steering (see p 291). An immature male canted to one side in an apparent response to the uneven strength of the deflection current in which he ascended; he stalled, his pitch angle leveled, and then he circled when the canted position became the banking angle of a turn. Slight differences in the angle of incidence between the two full wings should provide the bird a powerful means for turning, although it would be difficult to detect by an observer. That this technique may be employed either alone or in implementing other steering methods is suggested by three photographs of condors under special light conditions where the angle of incidence between wings can be seen to differ (Plate 29). With slow motion cine film, I found the angle of incidence along one full wing of a landing adult varied momentarily as the wing rotated forward and then back again. The other wing appeared to remain stationary.

Heading

In heading, the long axis of a condor flying in a crosswind is upwind from the flight path relative to the ground. The degree of this rotation or the angle of heading is a function of the velocity of the bird and the wind. I recorded the angle of heading for 47 condors crossing the observation beach, where velocities of bird and wind were known, and compared them with expected values computed in a vector analysis. For each observation, I used data on the velocity of the wind and the bird relative to the ground to compute estimates of the speed of the bird relative to the air and the direction of the relative wind. The expected heading angle was calculated as the angle between the direction of the relative wind and the flight path relative to the ground. Correlation between expected and observed values was highly significant (Figure 44). I did find, however, that a significant number of expected values were larger than those of the observed (34:13).[6] The flight path often passed slightly upwind of my observation point, and many condors turned their heads to the downwind side and watched me as they flew by. The steering effect of this movement would reduce the heading angle and probably accounts for the general difference noted between observed and expected values.

Double-Dipping

Description

The double-dip, another term from Hankin (1913), describes a common maneuver, the synchronized lateral movements of the two wing manus from the level gliding posture to a vertical position and their subsequent recovery (Plate 23, Figure 45). Momentarily, in the vertical position, the primary feathers of the condor assume the inward curvature characteristic of the pinions at rest and then again resume the outward and upward curvature typical of gliding flight, when the manus reach the horizontal plane of the body during recovery. At the onset of

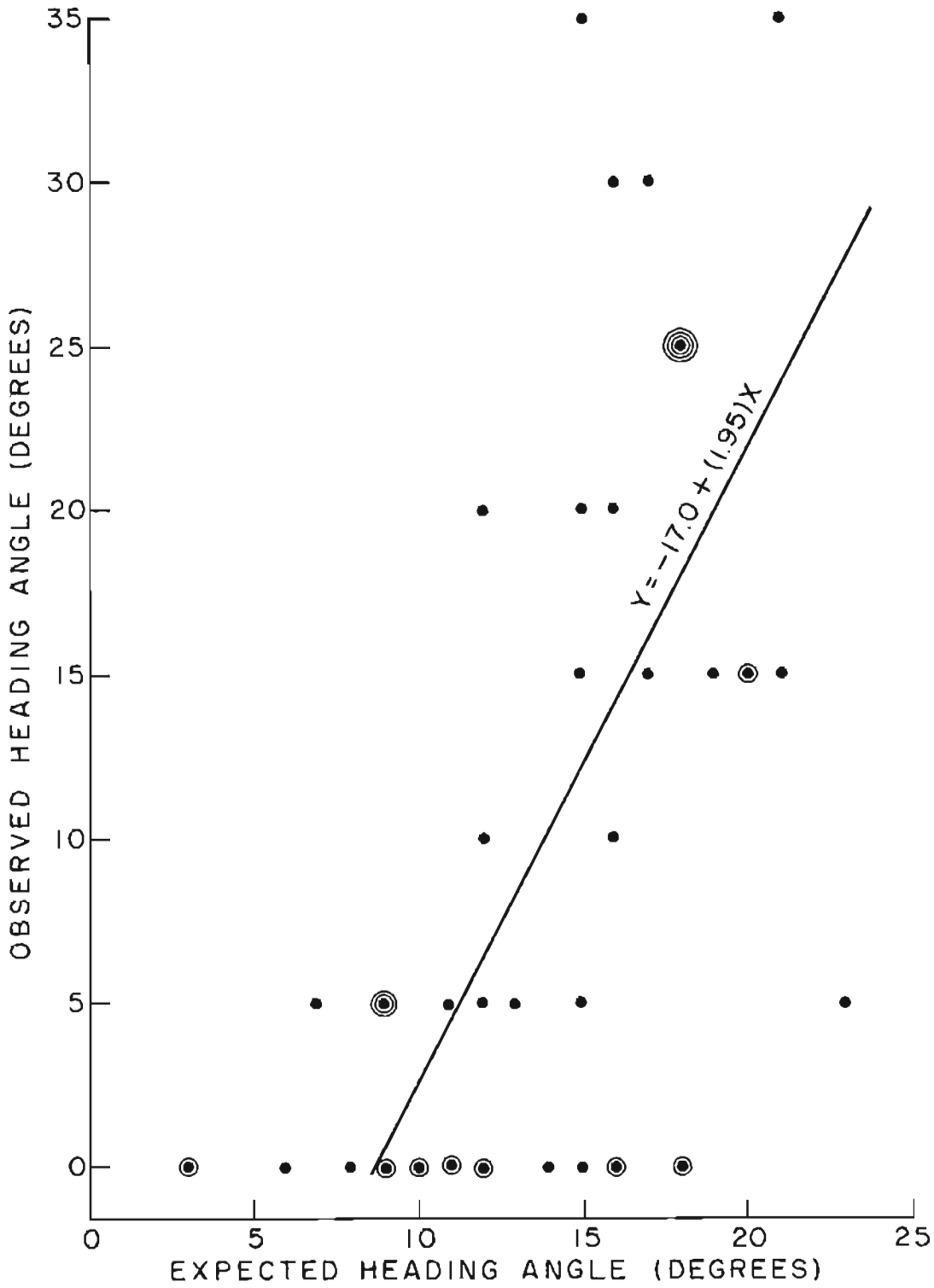


Figure 44. Observed heading angles compared to expected values calculated with data on forward airspeed of the condor and the speed of the crosswind (n=47, r=+0.83. p<0.001). Data recorded at Playa Chucho, Peru.

Plate 30. Condors in double-dip flight posture.

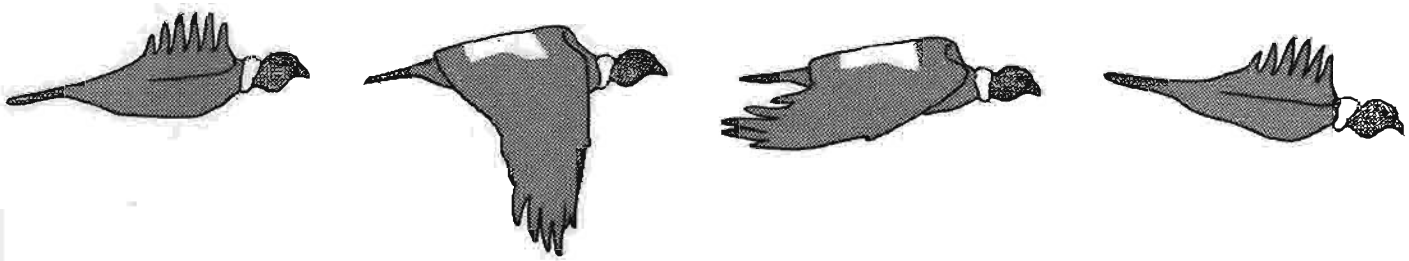


Figure 45. Four stages of the double-dip maneuver. Note the depression of pitch.

recovery, the primary tips move rearward up to 30 cm as the manus flex partially through a sagittal plane. After recovering through the transverse plane, the manus may assume a posture somewhat more flexed than that prior to the dip. The forearm and the brachium of each wing appear to move little during the dip; the forearm may move slightly toward the anterior. The pitch of the body drops forward during the recovery. The original and usually horizontal position of the body's long axis rotates downward as much as 35^{o}. I saw one dipping condor momentarily lift the tail about 15^{o} above the usual position during the rotary motion of the body. Subsequent to the change in pitch, dipping condors lost altitude and accelerated speed forward. Sometimes after dipping the condor gradually leveled in flight, decelerated, and dipped again. One condor double-dipped three times in 25 seconds; another bird dipped six times in 51 seconds in a rhythmic variation of speed and direction of descent.

In some isolated cases, the pattern of the dip varied. Some birds double-dipped while flex-gliding with lowered legs. Immature bird often wavered slightly from side to side during the dip; the duration of the maneuver seemed shorter than that of the adults. When I yelled at and frightened two adults, they both dipped spasmodically, flexing both wrists and elbows quickly; they lost altitude immediately. Dip movements were abbreviated, with the manus moving only a fraction of the distance to the vertical position. No distinct elements distinguished a weak double-dip pattern from that of a strong arching motion. In most abbreviated dips, the manus moved anywhere from 40^{o} to just below the horizontal plane; the primaries curved downward, and then the manus recovered. Four durations for full dips timed from cine film ranged from 1.0 to 1.5 seconds. Durations of abbreviated dips appeared to be no less than those of the full movement. The downward dip and the upward recovery motion were of approximately equal durations, separated by a pause at the nadir of the wingtip movement.

Context and Function

The double-dip pattern was consistently present in certain flight situations and absent in others. I never saw condors double-dip while crossing the channel from Isla Zárate to Punta Zárate nor when they crossed the observation beach. In both places, updrafts were probably minimal or absent. In Colombia, dipping was less frequent during misty and rainy days. Condors frequently double-dipped (1) at the onset of a flex-glide following a circling ascent, (2) after taking off from an elevated perch, (3) during steep descents prior to landing, (4) after suddenly encountering a sharp updraft, and (5) after stalling. Generally, dips following take off from cliff perches were abbreviated. Sometimes, when different types of extended and flexed flight postures characterized circling in one area, condors double-dipped in bouts. I saw a condor double-dip during a circling ascent only once. In general, the double-dip pattern is associated with situations where air conditions are changing, updrafts are present, and descending flight paths present no risk and, in fact, are sought.

The maneuver apparently provides a rapid means of accelerating and/or changing the angle of attack. During wing flexion in this pattern lift is lost or reduced, the body rotates forward, and the bird accelerates downward. The wings can recover into a configuration with a new lift-drag ratio providing a desired angle of descent. Although the condor can flex the wings or rotate them to different angles of incidence to obtain the same effect as the tip, the response probably has a time lag. The effect of a dip is immediate. Also, the double-dip, in accelerating the bird, may provide a gradient of air speeds that improves the condor's ability to test, sense, and select a proper trim.

Arching

In this rarely seen flight maneuver, the wing flexes slightly across the vertical plane cutting the span (Figure 46). Viewed from the front, the leading edge of the wing, straight in normal gliding flight, changes to an arch (wings in Plate 29 center may be slightly arched). In

Figure 46. A gliding condor with wings in the arched posture.

the arched position, the primary feathers continue to curve upward. Arching and flex-gliding patterns are viewed in different planes, so it is difficult to secure much data on the relationship of the two patterns during posture changes. Twice, I did see flex-gliding condors arch both wings. In an inspection of slow-motion cine film condor flight, I found, however, that most birds usually arch their wings very slightly, if at all, while flex-gliding.

Arching seems to reduce lift. Five different times I saw condors arch the wings, and an accelerated descent followed in every case. After ascending rapidly in circles of small radii, an adult female arched her wings and descended 200 m in a circling path. Arching seemed to be the only difference in her postures of ascent and descent. A female condor and a turkey vulture slightly arched one wing, and each bird, subsequently, turned to that side. Apparently, lift loss from arching caused the turn. Another female gliding in a declivity current near a cliff face flew with a slight arch in the wing nearest the cliff. The primary feathers on that side were bent upward less steeply than those of the outside wing. The vertical component of the wind may have been stronger nearer the cliff, and the condor, in arching one wing, compensated to maintain level flight.

Arching probably affects lift production and parasite drag force minimally and obtains most of its effect by increasing induced drag forces. An examination of cine film and photographs of condors in flight showed that the angle of incidence always varied along the span in a specific pattern: The angle is largest in the region of the proximal third of the wing and smallest in the narrow band between the wrist and the point where the primaries bend upward (Plate 29). Induced drag is minimal when the vortices developed by lateral currents produce air movement that is constant along the span (Prandtl and Tietjens, 1934, p. 204). The specific differences in the angle of incidence along the condor wing may operate to maximize the uniformity of air velocity at the trailing edge. If so, arching would increase induced drag by

altering these angles.

Moving the Feet

Frequently, condors in flight lowered their feet from the usual location beneath the tail into a zone that extended forward to a vertical position where the legs, protracted completely, hung at right angles to the body axis (Plates 27 and 31). Tarsi were not flexed. Generally, both feet moved in synchrony. In the elevated position, the feet may have buttressed the tail; the feet of one adult male extended through and above the tail in a gap where central feathers were missing (Plate 32). Sometimes when legs and feet were extended vertically, however, the tail moved to an angle slightly above the long axis of the body (Plate 31, middle left). Because the forward position of the feet may have operated to depress the pitch angle, by changing the location of the center or gravity, the wings may have advanced as well, to produce an opposing torque that would maintain a certain pitch. I often saw feet lowered for extended durations of many minutes in circling, gliding and flex-gliding flight and in ascents and descents. During single and double-dip patterns by these birds, the feet remained lowered. The posture usually occurred during flight in a small area with strong vertical updrafts. I did not see lowered feet in (1) early morning flight, (2) on long instance flex-glides, (3) while flapping in level flight, or (4) during any of the traverses recorded across Playa Chucho or the Zárate channel, where updrafts were reduced or absent. After circling within the Rio Pasto canyon, condors with lowered feet raised them back under the tail when they ascended above the rim and began a journey over an extended distance. Lowering the feet was usually the first indication that condors circling above our Colombian baits were about to land.

Contextual data for instances where wing flexion and feet lowering occurred together suggested that the legs and feet functioned as airbrakes. Pennycuick (1960, 1971b) monitored drag increases for lowered feet by flying fulmar petrels and Rüpelli's griffon vultures to

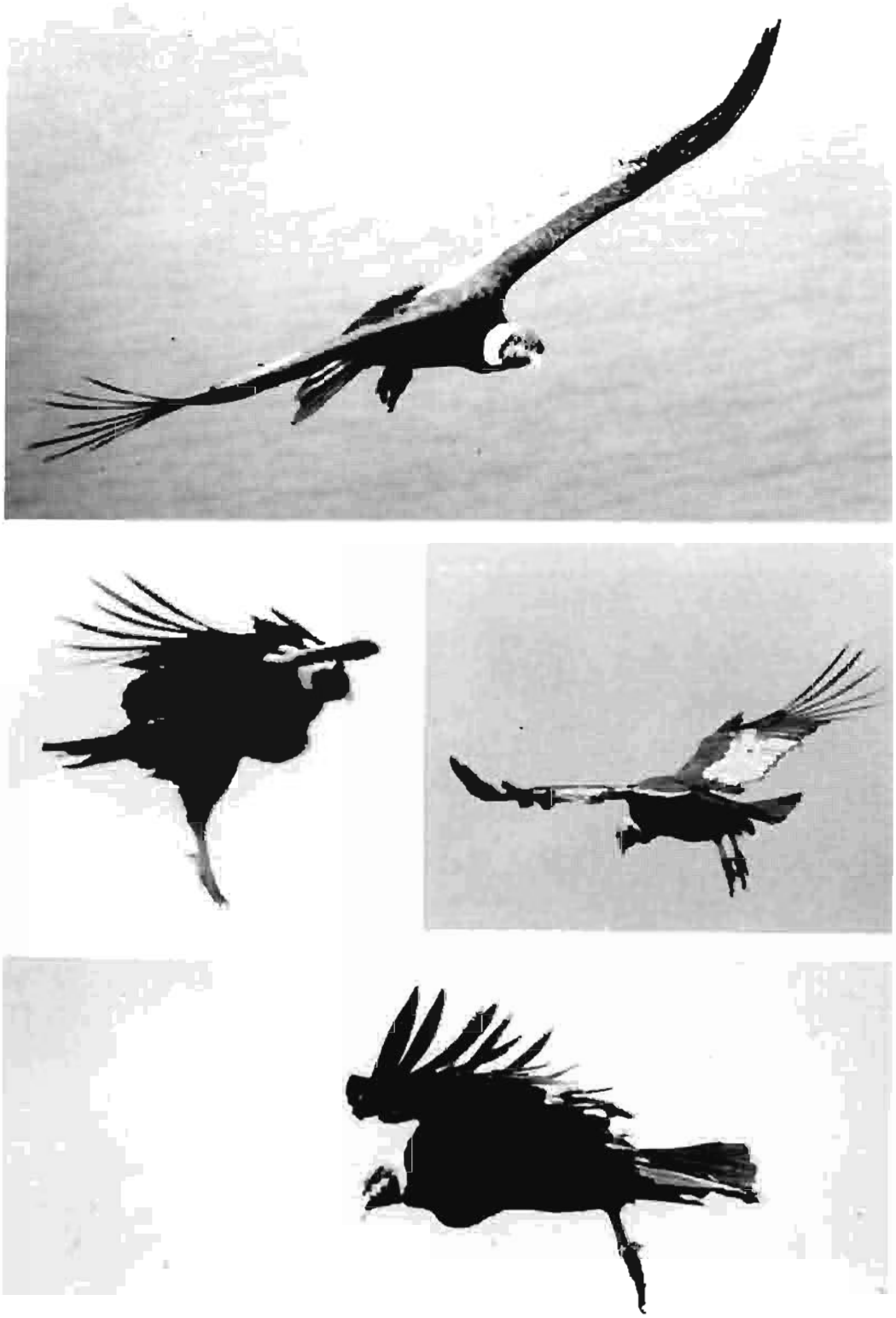


Plate 31. Gliding postures with the feet lowered.

Plate 32. A gliding adult male. Feet show through the gap in the center of the tail.

demonstrate airbrake action of the posture. Possibly, the posture also provides more stability in turbulent winds by lowering the bird's center of gravity relative to the wings.

Taking off

Take-off patterns from cliffside perches were rather consistent in form. The condor dipped forward so that the long axis of the body moved to a position about 35^{o} above the horizon (Figure 47). Simultaneously, the heel and knee joints flexed as the bird crouched and the brachia and forearms extended up and out. Then, as the legs straightened, thrusting the bird forward, the manus extended upward and into the same position assumed by wings recovering in a normal wingbeat. As the toes left the rock, the wings moved downward across a path similar to the wingbeat path of level flapping flight (Plate 33). Occasionally, condors leaving a cliffside perch flapped their wings in one or two abbreviated cycles or double-dipped slightly once or twice. Infrequently, condors left the perch without flapping or dipping their wings, holding them in a gliding position either extended or slightly flexed. Twice, I saw condors flap several times before their feet left the ledge perches. Sometimes they extended their wings and held them motionless for up to 30 seconds before taking off. Usually, the legs were elevated back under the tail shortly after leaving the perch. When condors flew from level ground or from gentle slopes, they usually flapped their wings in longer bouts and bounded over the ground in an upwind direction. Initial wingbeats in the bouts seemed reduced in amplitude compared to those after the bird was airborne.

Condors at feeding sites often climbed uphill before take off. One adult female condor with a very full crop climbed up a slope of about 20^{o}. She opened her wings and then after a pause ran downhill flapping for 5 m; she bounded three times across an additional span of 10 m before finally becoming completely airborne. Occasionally, I saw turkey vultures and black vultures with full crops climb uphill prior to take off. I saw an adult male and female each take

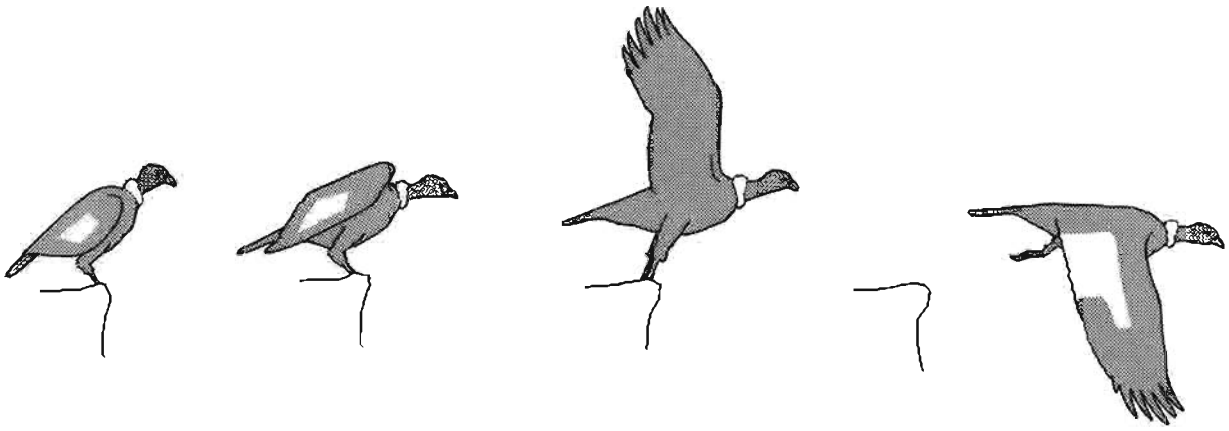


Figure 47. A condor taking off from a ledge perch.

Plate 33. An adult male taking off.

off from a hilltop by running with extended wings about 1 m into a steady wind. Neither flapped. An immature male startled on the side of a gully flew to the other side flapping 22 times, landed, wheeled around, and flew again. I saw a group of black vultures follow the same pattern. Apparently, by landing and turning, the birds were able to ascend more rapidly in escape from the gully without sacrificing efficiency on a sharp aerial turn.

Maximum ascent rates powered by energy of the bird alone are reduced for condors compared to other birds. The take-off path of a frightened female condor, ascending to escape, crossed a small climbing angle of only 3°30' (Table 74). She ascended at a mean rate of 0.7 m/sec, compared to 2.5 m/sec recorded for the pigeon (Pennycuick and Parker, 1966).

In a sequential analysis, I found that take off was often preceded by a bow stretch or by a body shake (Figure 12). Activity by the bird, in general, intensified before take off; significantly more major body movements occurred in the 5-min period immediately preceding take off than in the penultimate period of the same length (Table 79). Major body movements occurred in only 17 of 73 penultimate periods, compared to 41 of 73 periods just preceding take off. No significant differences were found in a similar comparison between activity levels of the second period with those of an antepenultimate, 5-min period.

Landing

Description

To land safely condors must reduce their speed relative to the ground. A unique wingbeat pattern that acts to reduce both sinking and forward speed characterized most landing maneuvers (p. 268). Before this pattern appears, the gliding bird often alters the pitch of the wings and body in a rhythmic motion. These oscillations in pitch may result from torques produced by moving the wings across a horizontal plane first fore and then aft relative to the center of gravity. Usually one or two of these patterns of pitch oscillation precede the first

Table 79. Variation in activity level in consecutive periods before take off.

Number of major body movements observed during period[a]	0	1	2	≥3
No. periods tallied				
10 to 5 min before take off	56	12	4	1
5 to 0 min before take off	32	23	8	10

$X^2 = 18.69$, $p<0.001$

[a] Posture changes, stretching, scratching, defecating, body shaking, and head wiping.

wingbeat, which is reduced, and then fuse with the flapping pattern in the same rhythm. Pitch increases as the wings stroke down and forward and decreases again during wing recovery. Generally, each succeeding wingbeat becomes more pronounced until after two or three cycles the pattern stabilizes (Figure 34, Plate 34). Sometimes the full pattern appears immediately with no gradations preceding. For 16 landing patterns when the condor flapped, the total number of reduced and full wingbeat cycles ranged from three to seven with a median of four.

During landing maneuvers, the tail is fully expanded and moves in harmony with the wings. In the downstroke, the tail is depressed so that the ventral surface thrusts forward in a direction opposite to the flight path. During wing recovery, it is elevated across an arc of 30^{o} to 40^{o} to an angle above the long axis of the body. Active muscular control of the tail in this movement is probable, because the angle of oscillation exceeds pitch changes by the body. I did not detect, however, any regular changes in the degree of tail expansion during the landing maneuvers. Just before alighting, usually before the last two wingbeats, the legs are extended forward and the toes spread. While the long axis of the body moves from about 30^{o} to 45^{o} with the horizon, the legs extend to a position roughly perpendicular to the body. Contact does not occur at any particular phase of the wingbeat cycle. When landing on the flat ground near the baits, the condors usually bounded once after landing. Upon contact, all leg joints bend and then extend together to produce a hop that usually carries the bird 10-20 cm up and 40-50 cm forward. Generally, most of the wing folding occurs during the hop so that, when the condor pauses immediately afterward, both wings have already been retrieved.

Patterns for Different Landing Sites

Motor pattern used just before alighting did not vary much according to the type of landing site. The position of the legs relative to the body and the pitch of the bird seemed to be the same for patterns of landing on either flat open ground or on cliff ledges. One difference

Plate 34. An adult male landing.

appeared to be the presence of a greater forward velocity before contact by birds alighting on cliffs and a greater sinking velocity for those landing on open ground. Condors landing on cliffs decelerated more before landing and did not bound after contact.

Although final landing patterns for open areas and cliffs were similar, approaches to these different sites varied considerably. Condors circling over open level areas near the study baits usually initiated landing approaches by lowering their feet; then, in long flight paths across shallow angles of descent, they glided with either flexed or extended wings upwind toward the landing site. Condors alighting on narrow cliffside perches, however, almost always flex-glided with lowered feet in steep S-shaped descent paths to some point below the perch site, where they extended their wings and rose sharply in a decelerating ascent that carried them to a stalling point near the level of the perch. Usually, each turn in the approach directed the condor toward the cliff, although occasionally they spiraled downward, completing one or two circles before turning again to the other direction. Some turns were so sharp that the span axis of the bird became almost vertical. One typical approach began 100 m almost directly above the perch. The condor descended in a series of five sharp turns to a level 15 m below the perch, where he opened his wings, increased his pitch, and shot up to the ledge. Again, in a 100-m descent, another condor that turned 10 times from one side to another never completed a full circle in a spiral. Although I saw a few condors descend slowly with a positive pitch angle, most descended rapidly with a negative angle.

Ascending condors often passed by a perch, only to descend and land after rising some distance above it. I saw an adult male approach, ascend on by, and then descend to land on a perch, even though his circling ascent was very gradual and interrupted by several flapping bouts; marginal conditions for ascent seemed less important than a descending approach. Such an approach to a perch of small size may function in much the same way as the steep descent

used by pilots to land on small airfields or aircraft carriers. Compared to gradual descents covering longer horizontal distances, the more vertical approach places the bird or airplane nearer the landing target at any given altitude, so corrections in the flight path can be more accurately made.

Variation

I noted some exceptions to these general landing patterns. I saw one condor land on a cliff after a long descent across a shallow glide angle in an approach that never ascended above the level of the perch. Another bird circling in the rain landed on a cliff perch without ascending above it. Eight condors landing at a coastal roost in strong and turbulent winds all approached the cliff from a point below the perch and about 200 m distant. Each bird moved directly but slowly toward the cliff; they wavered from side to side and gained altitude gradually. Within a few meters of the cliff, they flapped and landed gently. The strongest vertical currents appeared to be nearest the rock. In northern Peru, I watched a condor descend rapidly, then glide along a level flight path, gradually decelerating as he neared a long ridge. He landed on the ridge by decelerating as he neared a long ridge. He landed on the ridge by decelerating until motionless relative to the ground, lowered his legs, and touched down with a single wingbeat. A condor landing in brush 2 m high and with cover of about 70 percent ceased forward motion just above the vegetation by increasing pitch and stalling; then he flapped four times and descended vertically into the brush. He held his head down below the plane of his body. In Colombia, condors frequently landed on epiphytic bromeliads growing on the cliffs, and I once saw the plant break loose when the condor landed; he dropped off to the side and sailed out again. Four times, I saw condors stall in the decelerating ascent before reaching the perch site. In each case, the bird single-dipped, turned, flapped once or twice, and descended out away from the cliff. Immature condors often did not land as smoothly as adults. Frequently, they swayed from side

to side just before landing and alighted off balance with legs splayed apart.

Other Maneuvers

Maneuvers in Pursuits

Patterns of Pursuit. An aerial pursuit usually began when one flying condor suddenly descended toward another; generally, the diving bird flexed both wings (almost completely sometimes), assumed a sharp negative pitch angle, and accelerated downward along a flight path that often approached the vertical. I saw an adult dive 200 m vertically to pursue an immature bird circling below.

In these pursuits, the lower bird usually dove in a similar manner and maneuvered sharply in turns of alternating direction by single-dipping one flexed wing and then the other. Successive dip movements were often strong enough that the span axis of diving birds neared the vertical following each dip. From the side, an observer could see in rapid succession, first, the belly and then the back of the bird during the weaving descent. The bird in pursuit, following the maneuvers of the pursued, matched each turn; except for a very slight time lag in the action of the pursuer, the two condors seemed to move in synchrony, executing full and frequent turns at high speed.

During more level phases of extended pursuits, however, the flight patterns of the two birds often differed in three ways: (1) The lead bird frequently flapped, while the other did so rarely. In four instances when the pursued flapped more than the condor behind, the distance separating them increased. (2) Occasionally, when a pursuing condor passed over and beyond the other bird, the pursuer stalled momentarily, ascended and decelerated to zero velocity, and then, usually after a double-dip, descended in pursuit once more. I also saw this maneuver in pursuits between black-bellied buzzard-eagles. These patterns probably acted to re-establish the position of the pursuing bird above and behind the other. (3) Pursuing birds often lowered their

feet; pursued birds did so rarely. In one pursuit and adult male with lowered feet chased an adult female with elevated feet over a 2 km in a fast and straight descent. The flight posture with lowered feet acts to reduce the glide angle and may help prevent the pursuing condor from overshooting the other bird. I saw one adult dive at an immature bird and pass beyond in front of the young bird. The adult ascended sharply, stalled, and then lowered both feet while descending. In the interim, the immature bird emerged below, and the adult dropped down upon the young bird again. In some instances, the pursuing condor extended legs and feet momentarily in an apparent attempt to strike the other bird. In two separate instances, I saw an adult male dive at an immature male, lower his feet, and strike the young bird on the back with his feet. In one case, the force of the blow appeared to knock the immature condor downward 6 to 8 m. One adult male plunged toward another perched on the ground and narrowly missed striking him with lowered feet. At a Peruvian feeding site, a flying adult male pursued an adult female in take off flight. He struck her in the back with both feet and bit toward her neck but without making contact.

Pursued birds flew evasively; sometimes they moved the feet or beak toward an approaching bird. Twice, I saw pursued immature condors roll to one side into an inverted position and throw their feet upward toward the approaching adult. In each instance, the adult did not strike the immature condor, and the young bird resumed normal flight with the feet elevated beneath the tail. Occasionally, a pursued condor stretched his neck up and directed an open beak toward the bird above (Plate 35). An immature male did this and stalled; he flapped five times before regaining equilibrium. If the pursued bird ascended above the other, active pursuit ceased. Either the two condors flew in separate ways, or they circled together until the pursuing condor ascended above the other bird, and the pursuit continued.

Plate 35. An immature female (below) pursued by an adult male (above).

Prolonged pursuits. I saw a few extensive pursuits. In one unusually long one, an adult male chased another adult male in three long cross-country bouts, 2, 12 and 1.5 minutes in duration. The bouts were interspersed with two periods of circling, 2 and 1 minute in duration, respectively. After crossing over about 18 km ground distance, this chase ended when the pursuing condor turned and glided back toward the area where the pursuit began.

In the Colombia study area, pursuits regularly led to the lower part of the Rio Pasto canyon. Although prolonged chases continued there, flight patterns changed; dives by both birds became shorter and less steep. Usually, after each dive, both birds ascended sharply, almost to the stalling point, and then circled for a short period before plunging again. Sometimes both ascended up to the canyon rim in this manner. The pursuing condor in these ascents approached the other more closely than in the long steep dives.

At Paracas, in a 10 min chase restricted to one general altitude level above the sea, two adults flapped in many long bouts. Periodically, the flight paths seem to extend beyond the range of the deflection currents, so that flapping was necessary for maintaining altitude. Sometimes pursued condors, mostly immature birds, landed during a chase. Usually, the pursuing condor then landed or began to land at the same site, the perched bird flew, and the pursuit continued. Once, when an immature bird alighted, two adults in pursuit began to land there simultaneously; when the younger bird took off, the three nearly collided.

Maneuvers for Stability

Wing Flexion. Wing flexion may counteract forces that tend to roll the bird. I saw a condor tossed about in turbulent wind flex both wings slightly, descend about 6 m after his pitch dropped to a negative angle, and then extend his wings again. In a moment, buffeted again, he repeated the pattern, apparently to secure a momentary stability in the flexed posture. Despite stalling effects indicated by fluttering coverts, flight apparently stabilized with the increased

weight-loading ratio of the wings.

Changes in the dihedral angle. Condors usually glided with both wings in the same horizontal plane but in turbulent winds, I frequently noted an angle of about 170^{o} between the dorsal wing surfaces, a dihedral angle of about 85^{o}. This angle would provide more stability in turbulent air also by counteracting rolling forces. Suddenly canted to the side by a gust, the lower wing of the rolling bird produces a larger lift component in the vertical direction than does the sloping upper wing. The resultant torque tends to roll the bird back to the original position. In these turbulent winds, I noted repeatedly that the tail bowed laterally and matched the angle changes in the wing plane, perhaps to function in a similar manner.

Several other observations suggest that a reduced dihedral angel of the wings might have a function associated with surplus weight. Two adult females and an adult male circled over a bait in Colombia. Unlike the females, the male had a full crop and his wings were held slightly above a level position. An adult female with a full crop flapped 32 times while crossing Playa Chucho in a 6 kph crosswind; a dihedral angle of about 85^{o} characterized her glide posture in the wingbeat intervals. When four adult males crossed together, one with a full crop held his wings with a dihedral angle of about 85^{o} during the glide intervals between bouts of flapping. The other males had empty crops, did not flap, and held their wings in a horizontal plane. Wind speed was 12 km/hr. Airflow above the beach, as judged by smooth flight of the traversing birds, always seemed even. Perhaps condors do not attempt to soar with level wings when additional weight places an extra stress on the pectoralis muscles or bone structure of the breast. Although some relationship may exist between crop loading and dihedral angle in some situations, my records for condors crossing the Zárate channel indicated level wing postures for all gliding intervals between flapping bouts, regardless of differences in crop content among the birds.

Adult— immature comparisons. The flight of immature condors seemed less stable than that of adults. Younger birds wavered from side to side in double-dip maneuvers. Single-dip patterns usually occurred in pairs; the second, on one side, apparently compensating for an excessive movement by the first, on the other. Immature birds rotated their tails in larger angles than adults did. Occasionally, young condors alighted off balance, whereas adults did so rarely. After stalling, one immature bird flapped five times, apparently seeking a proper pitch; adults usually double-dipped after stalling and then leveled out in stable flight.

The difference in profile of adult and immature wings (Figure 48) is of note here in comparing the stability of young and adult birds. Wings of the younger birds are comparatively wider. Presumably, profile changes during maturation sacrifice relative stability for maneuverability as the bird gains more experience. The longer chord lengths should allow younger birds to fly more slowly, with steeper angles of attack, without stalling. If, for example, the boundary layer detached from the condor wing during conditions defined by a Reynold number of 2.28×10^5, minimum speed for an adult with an average chord length of 38 cm would be 0.9 m/sec; for the immature bird with an average chord length of 38.5 cm, the stalling speed would be 8.9 m/sec, assuming the kinematic viscosity remained constant at 0.15 cm/sec (equation 6). The difference seems negligible. However, the major difference in chord length is restricted to one area in the proximal part of the wing. Possibly, maintenance of optimal flow conditions in this region, relative to that of other wing areas, is more essential to stability. Considering differences for wing sections with maximum chord lengths, I computed in the manner above a stalling speed of 7.3 m/sec for a wing section, with an adult chord length estimated at 47 cm. For a comparable wing section of an immature I obtained a stalling speed of 6.6 m/sec, with an estimated chord length of 52 cm. Perhaps a reduction in stalling speed for one part of the wing, estimated here at about 10 percent, is significant in maintaining stability.

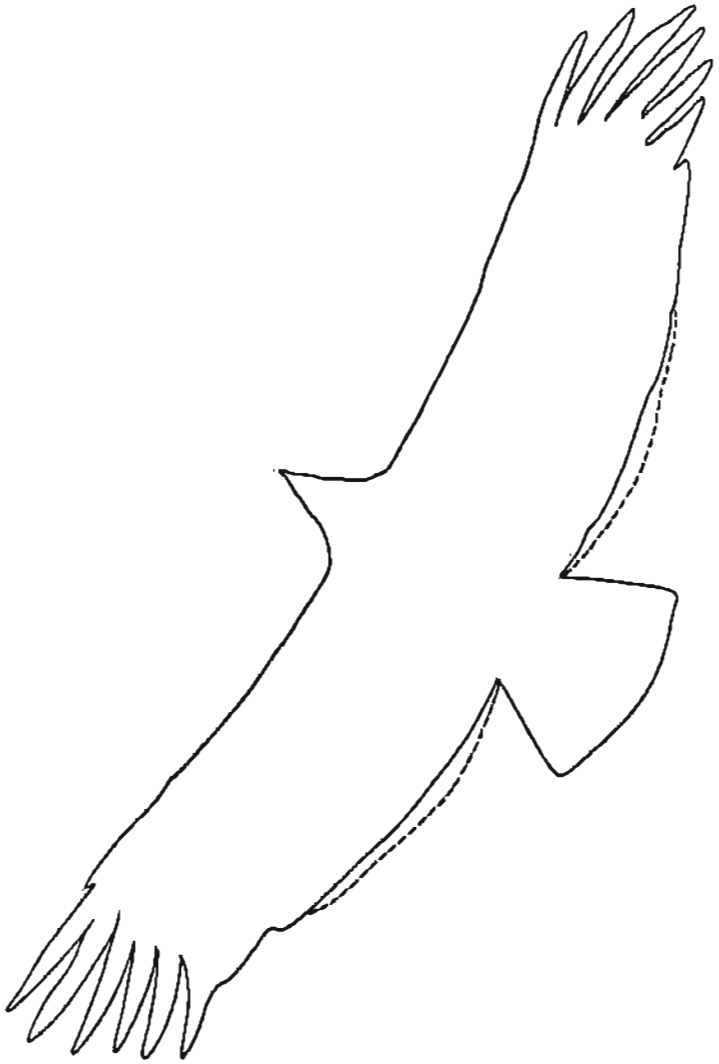


Figure 48. Differences in the gliding profile of an adult and an immature condor. The dotted line indicates the wing profile of the immature bird. Taken from photographs.

Activities in Flight

Most of the activities observed for flying condors involved preening. On seven different occasions, I saw flying condors make preening movements on the neck, breast, or patagium region of the wing for durations of 2 to 15 seconds. Usually, pitch increased and forward speed was checked during the activity. Most of these observations were of condors gliding in slow ascent or descent in strong deflection currents. Wings were either extended or partially flexed. One adult male, while preening the ventral neck region, glided on fully extended wings with his feet lowered. An immature male nibbled at his breast, neck, and then at the leading edge of the wing in the wrist region. He flexed that wing slightly, canted, and turned to that side before extending it again. An adult female in a strong deflection current ascended and glided backwards for several moments while preening her neck and shoulder area. Several times, I saw condors increase their pitch and almost stall while extending the neck up and directing the head back, apparently to look behind. Other condors were flying behind them at the time. I saw a gliding adult female defecate, and in three other separate instances I watched an adult male scratch his head while gliding (Figure 7).

INFLUENCE OF ENVIRONMENTAL VARIABLES

Wind-Topography effects on specific maneuvers and local flights

In Colombia, roost-departing condors paralleled the canyon escarpments at a distance of 20 to 40 m. In traversing a ravine on the canyon wall, the flight path usually curved in and out parallel to the contour line at that altitude, so the distance between bird and ground remained somewhat fixed. Morning updrafts were probably strongest in that band. One misty morning, I saw a condor in flapping flight descend while crossing the canyon; after turning and gliding downriver along the other side, he did not flap at all and descended less rapidly. Morning routes

along the canyon usually led to a particular area, where the bird began circling.

Topography-related patterns of flight were also evident in the Cerro Illescas mountains. In one instance, an adult female departed from a roost there and flew along a main ridge top flapping in intermittent bouts. At each of five different spur ridge junctures, she started to circle, but left the pattern only one-half to two-thirds complete before cutting across it in flapping flight and continuing on along the main ridge. Presumably attempting to ascend, the condor began circling each time at sites where the topography was similar; these sites were probably chimney-like in effect and produced columnar updrafts.

In Colombia, condors sometimes ascended in figure-8 patterns, with an exaggerated long axis oriented parallel to the canyon wall. This pattern usually occurred in front of broad flat walls, whereas circles appeared in more restricted areas like gullies. Against flat walls, the elongated pattern would be better than the circle, not only in providing prolonged exposure to a band of strong vertical airflow, but also in lessening the overall rate of descent with an inefficient banking angle. Unlike circular patterns, the figure-8 pattern did not seem to expend in size with altitude gains, but I did find, as with circles, that the bird ascended faster at higher altitudes. A condor 250 m from the canyon bottom, ascending in figure-8 patterns at a rate of 0.7 m/sec, accelerated to the rate of 1.5 m/sec when 600 m from the bottom.

Although the characteristic diel changes in air movement in the Cerro Illescas and the Colombia study area developed gradually over a period of hours, conditions permitting flight developed rapidly. Apparently, the range of minimum wind velocities critical for sustained flight is quite narrow. On one occasion an adult pair left a Cerro Illescas roost at 0920, and each bird flapped frequently in a descending flight path. They landed, waited 10 minutes, and flew again, this time ascending, even though they flapped less. In Colombia, I saw a black-bellied buzzard-eagle dive at a roost departing adult female at 0927. In averting the buzzard-eagle, she

descended 100 m though seemingly stable air. Then, in the same flight pattern and across the same area she ascended in 2 minutes the same 100 m distance she gained in a 8-min period immediately preceding—a fourfold increase in climbing rate within a 1-minute period.

In the Paracas area, the presence of flapping in flight was related to wind speed. In general, condors crossing Playa Chucho flapped when wind speeds were low and glided when they were high. When wind speed exceeded 15 km/hr, condors flapped in only 11 of 25 instances, compared to 31 of 32 cases when wind speeds were less, a significant difference.[7]

Apparently, the deflection currents of strong winds provided them with a higher initial altitude for crossing the beach, thus reducing the necessity to flap. Condors did not flap in 13 of 28 crossings when initial altitudes exceeded 50 m, whereas at lower altitudes only 2 of 29 did not flap, again a significant relation.[8] Initial altitudes recorded ranges from 12 to 74 m, with a median of 51 m. Sometimes condors gliding above 75 m were not recorded, but in each of the two preceding tests, this bias acted to retain the null model.

I found a significant positive correlation between the air speed of condors gliding across Playa Chucho and the speed of the wind, a crosswind at that location (Figure 49). For flapping birds, this relationship was not significant. By increasing air speed in a crosswind, gliding condors probably reduce altitude loss. At any given air speed of the bird, the time required to cross the beach is directly related to the crosswind speed. When gliding in a crosswind (or upwind), higher air speeds are necessary; air speeds that exceed levels providing a minimum sinking speed or glide angle ar useful in crosswinds, when less altitude is lost by trading a small increase in sinking speed for a reduction in flight time necessary to cross a certain ground distance.

Condors sometimes seemed aware of air conditions in the distance. I saw a female descending rapidly toward the sea as she glided along a series of cliffs. There, the wind blew

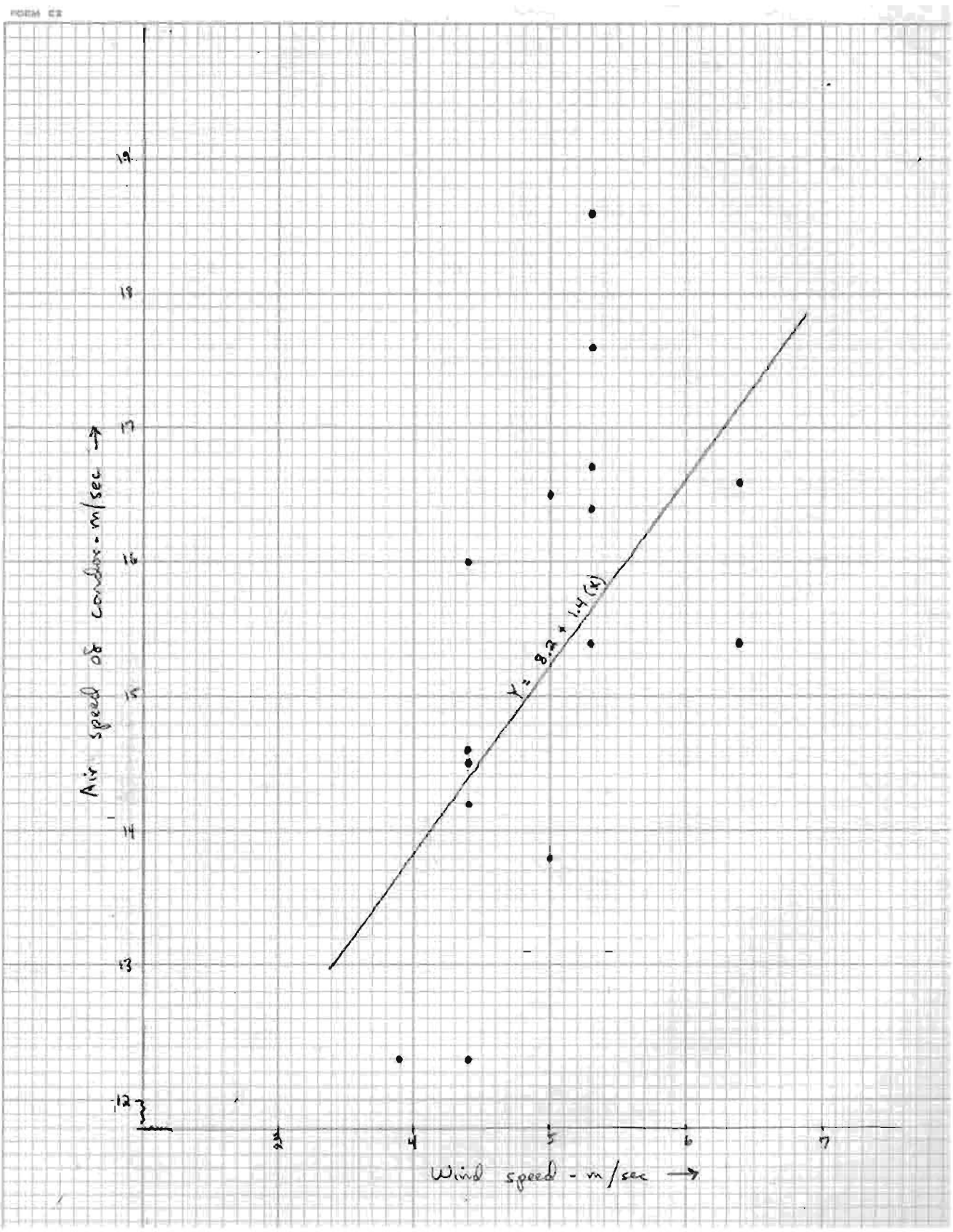


Figure 49. Air speed of 15 gliding condors related to speed of crosswind (r=+0.58. p<0.02).

parallel to the rock faces. She finally reached a set of bluffs facing the wind and, without a single wingbeat, smoothly ascended up away from the water in deflection currents apparently present there. Condors also seemed aware of the delayed and distant consequences of immediate maneuvers. I watched on bird circle to a high altitude (over 500 m) and then flap intermittently during the beginning of a long glide through relatively calm evening air. Reducing the sinking speed at that moment by flapping seemed of no immediate use. Presumably, however, the exertion served to advance the endpoint of the flight path in an area many kilometers away.

Wind—Topography effects on general foraging movements

Foraging in the Colombia Study area

In Colombia, condors foraged over large areas by alternating circling ascents and gliding patterns of descent. Typically, each of the flight patterns occurred in areas of a characteristic topography: circling along and above steep slopes and gliding over flat areas. Routes seemed fairly consistent from day to day. One pair (1) ascended out of the canyon at the same place every morning to begin foraging. The location, a concave palisade of cliffs nestled between the canyon wall and the downstream side of a spur ridge, apparently deflected and funneled daily mountain-and-valley breezes into vertical currents. Mist verified this impression; one morning at 0930, I watched mist in front of the roost cliffs drift at a scarcely perceptible rate toward the area where the pair usually ascended. There, mist moved vertically at an estimated rate of 30 cm/sec. One evening at 1757, the adult pair left the roost perch and pursued an immature condor. When they returned and glided on fully extended wings in front of the 1-km series of cliffs in the roost area, they both descended, presumably in response to the diminishing strength of evening vertical currents. Earlier, their flight paths in that location ascended. When they reached their usual site of ascent, however, both birds circled, gained 300 m, and returned to the roost.

Many routes used by condors seemed specific to individuals or pairs. In the morning,

after ascending out of the canyon, pair 1 almost always glided across a plain to one particular mountain, where a second ascent followed. Whereas pair 1 frequently glided over my observation point during the day, pair 2, roosting on the same series of cliffs, almost never did. Their usual approach to the roost cliffs was from another direction. Although many routes were used by specific pairs or individuals, some areas were visited by many condors almost every day. A ridge rising out of a flat expanse in the eastern part of the study area was a favorite site of ascent for a number of condors.

Early morning air was calm in Colombia; I never saw a condor in flight for more than several minutes before 0730. The Paracas area, however, was sometimes buffeted by dawn winds, and then condors were often aloft at daybreak. Once, in foredawn twilight at 0540, I saw a pair circling without flapping above a sea cliff in an 18 km/hr wind.

Foraging in the Paracas Area

Condors in Colombia used large-scale vertical air movement powered by local thermal conditions. Birds in the Paracas area seemed restricted to updrafts produced by cliff-deflected winds. The presence of a strong south wind on the Peruvian coast coincides with a general absence of local thermal air movement (Trewartha, 1966, p. 28). When I followed the progress of an adult male as he flew several kilometers into the desert, I noted that he flew just above the crests of low hills. When they ended at a flat, he wavered for 1 minute and then turned back to the coast by following the same path. I saw a condor fly from an island to the tip of the Zárate Peninsula, continue on above the cliffs along the southern edge to the peninsula base, and then suddenly turn north and downwind, cross the flat rapidly, and disappear along the coast heading north. Apparently, this bird facilitated his progress toward the north by first flying southeast to take advantage of the strong deflection currents on the windward side of the peninsula. Although flight on the lee side of the peninsula seemed less regular and less stable, condors did fly there in

routes restricted to an area below the edge of the cliff, where vortical movement apparently produced updrafts near the rocks. I saw an adult female flying there arch her wings and descend after rising up near the edge of the cliff. Strong horizontal currents at the cliff tops cap the updrafts, and apparently she maneuvered to avoid them.

Occasionally, updrafts from local thermal activity did seem to occur in the Paracas area. On days when the south wind was weak, I noted condors flying above their usual altitude of 50 to 100 m. On one cloudy warm morning, I saw an adult over Punta Zárate flex-gliding at an altitude of about 600 m; surface wind speed was 8 km/hr. Another morning in the same place, I saw a condor at an altitude of about 300 m, when the surface wind was only 2.5 km/hr. At the observation beach, I noted condors in the morning rarely flew above 75 m when winds were less than 15 km/hr, but in the afternoon, on those few days when wind speeds remained below 15 km/hr, birds frequently crossed at altitudes exceeding 75 m. One calm day, I saw a condor circle in slow ascent over the desert near the observation beach before turning toward it and crossing it at an altitude above 75 m. Presumably, on most days, the strong south wind leveled or tilted downwind any thermal updrafts (Woodcock, 1942).

Foraging in the Cerro Illescas Area

Unlike the linear foraging routes in the Paracas area, those of the Cerro Illescas condors wandered over large areas. Apparently using local thermal currents, condors in this desert range foraged much like the Colombian birds. Frequently, I saw them circling at altitudes of 1000 m under low compact cumulus clouds. Occasionally, they ventured out into the flat Sechura desert, an area presumably devoid of any significant deflection currents. I once saw a condor circling in the desert plain 65 km away from the nearest roost area. In a cave 13 km from the sea, I found a condor regurgitation pellet containing pelican feathers. Even on cloudy days, thermal updrafts were evident. On a calm morning at 1105, I saw three condors ascend while circling over the

desert 7 km from the foothills of the Cerro Illescas. The sky had been overcast but bright all morning.

Effects of Clouds, Fog, and Rain

Although thermal updrafts may exist on overcast days, several observations suggest that cloudiness does inhibit levels of thermal activity. Within one two hour afternoon period, a condor crossed, four different times, a 2 km flat separating the Rio Pasto Canyon from the Cerro Cuntur Ridge; the bird glided on the first three journeys and flapping on the last. The clear sky became heavily overcast after the third run and about 40 min before the last, when the flight pattern changed. In the second observation, a condor went to the roost on an unusually overcast day at 1734, a half hour to an hour earlier than normal for clear days. Houston (1974a) reported that overcast conditions limited foraging patterns by griffon vultures; these birds resorted to using deflection currents of one particular area during periods of heavy overcast.

Sometimes condors flew directly into clouds or fog. In the morning, they frequently circled in masses of fog within the confines of the Rio Pasto Canyon; in the afternoon, high flying birds occasionally ascended and disappeared into the bases of stratocumulus clouds. In fog at the edge of a Paracas bluff, I once saw a condor in a flex-gliding pattern remain motionless relative to the ground. In Colombia, I watched one adult female flap while circling in the fog. In a 10-min period, she ascended at a mean rate of 0.1 m/sec. Estimates recorded for the rate of ascent of mist in the Rio Pasto Canyon on one occasion ranged from 0.7 to 2.5 m/sec, while horizontal wind speed at my location on the rim, was only about 3 km/hr or 0.9 m/sec. According to earlier calculations (Table 75), a condor gliding in level flight would lose altitude if air did not ascend at a rate greater than about 1 m/sec. For circling flight, this threshold value would increase in an inverse relation to the radius of the circle.

Condors can fly in the rain. An adult pair circled for 2 min in a sudden but steady

afternoon rain, and both ascended slowly along the canyon wall. I saw one adult ascend slowly, circling in light rain, while another flex-glided in a steep S-shaped descent through heavy rain; both landed on rain-sheltered ledges. After a two-hour rain during the night and a light sprinkling rain in the morning, two immature males were still on the roost at 1035 when two men flushed them. Both circled in slow descent and landed below in the canyon. Then the sun appeared for the first time that morning, and both sunned. Flushed again at 1050, both ascended slowly at a mean rate of 0.5 m/sec. during a 9-min period.

CONCLUSIONS

The flight performance of condors and turkey vultures was evaluated by monitoring certain features of wind and flight whenever these birds crossed a certain Peruvian beach. Derived from a vector analysis with measurements of wind velocity and ground velocity of the bird, I obtained the following mean air speeds: 15 m/sec for 15 gliding condors, 14 m/sec for 42 condors that flapped during the crossing, and 10 m/sec for five turkey vultures that flapped. For the 15 gliding condors, I computed a mean lift coefficient of 0.7 and a mean induced drag force of 3 newtons. Implausibly low values derived for parasite drag coefficient of the condor seemed due to (1) unmeasured forces of deceleration and (2) an undetected vertical component of the wind at the level of the flight path. Field data, adjusted by introducing a coefficient of parasite drag determined for the black vulture in a wind tunnel study (Parrott, 1070), provided corrected estimates for both parasite and total drag. I secured an adjusted value of 14 for an estimate of the lift-drag ratio of a condor gliding with wings fully extended.

Flex-gliding postures usually characterized long straight flights and apparently acted to provide an efficient means for increasing air speed. A moderate flexion that reduces the extended span by 20 percent is estimated to increase the optimum air speed from 13.9 to 15.2

m/sec for an adult male and from 12.6 to 13.8 m/sec for an adult female. Modifications of tail area paralleled those of the wings; the tails of condors crossing Playa Chucho at higher air speeds tended to be less expanded. In strong deflection currents, marked flexion of the wings and lowered legs often characterized flight with a notably reduced ground speed. A reduction of the lift-drag ratio due to airbrake and stalling effects coincides with (a) an increase in sinking speed, which apparently is offset by the deflection currents, and (b) a decrease in forward speed.

In general, condors rarely flap in level flight; when they do, the bouts are short. In 175 bouts, the number of wingbeats ranged from 2 to 6, with a mean of 3.5. Wingbeat frequency recorded for level flight was 1.8 cycles/sec for the condor and 3.9 for the black vulture. A frame-by-frame analysis of movie film (64 frames/sec) provided data for a detailed description of the condor wingbeat in both level and landing flight patterns.

Flapping can provide both propulsive and lift forces. In level flight, however, at air speeds approximating those of equilibrium gliding (14-15 m/sec) flapping reduces sinking speed without accelerating forward air speed; at these air speeds, flapping appears to retard forward motion. I used average estimates for speed and direction of the wind striking a flapping wing during four phases of a wingbeat cycle to examine a system where a multitude of forces change in magnitude and direction every moment. These estimates suggest that the flapping wing of a condor increases lift forces by accelerating the speed of the air striking its surfaces and by twisting simultaneously to present airfoils with optimum orientation toward the changing direction of the resultant relative wind in both the down-and upstroke. Positive or negative components of lift and thrust forces are produced in various combinations, depending on the angle of attack. Thrust forces appear when air speeds of the bird are less than those of equilibrium gliding, a normal condition in take off. The average velocity of the resultant wind striking the wing is greater during the downstroke than the upstroke because of the anterior slant

of the downstroke axis. Mechanical efficiency of the lever system operating in a wingbeat is greatest during the downstroke, so this orientation is important for producing maximum lift forces.

Condors crossing Playa Chucho tended to flap when wind speeds were reduced ($\leq$15kph), but glided when they were high. Apparently, deflection currents of strong winds provided them with a higher initial altitude for crossing the beach and reduced the necessity to flap. Air speed of the gliding condors was directly related to the speed of the crosswind. Presumably, the birds lose less altitude in a crosswind by trading the small increase in sinking speed accompanying increased air speeds for a reduction in flight time necessary to cross a certain ground distance.

Condors seem to be incapable of extended flight without vertical wind currents. The minimum power output required for sustained flight in still air was estimated to be 33 watts/kg wing muscle for the condor and 190 for the turkey vulture. The minimum power output generated by a startled condor in escape flight was estimated to be 54 watts. Assuming (a) the ratio of power output for exceptional and sustained efforts by human muscle (40:17) is similar to that of the condor and (b) the mechanical efficiency of flight systems for exceptional and sustained efforts are similar, approximately 23 watts/kg wing muscle are available for sustained flight by the condor, only about 70 percent of that estimated as necessary.

With data from a regression analysis relating flapping rate to sinking speed, I calculated that about 160 wingbeats/min are required for the condor to maintain level flight, whereas only around 75/min are needed for the turkey vulture. Two factors of dimension probably account for the difference: (1) weight loading of the turkey vulture wing is about half that of the condor, and (2) wing muscle composes a larger part of the body mass in the turkey vulture.

The slotted wingtips of the condor are well suited for producing substantial lift forces on

a steep glide angle in a reduced relative wind, two constraints characteristic of circling flight. I measured the banking angle and the size and duration of 11 circles by two adult male condors in slow ascent and secured lower and upper estimates of 5.6 to 7.2 m/sec for forward air speed. Resultant air speed must be greater in equilibrium gliding. To see if these low forward speeds were augmented by a high sinking speed in rapidly ascending air, I assumed lift coefficients of 1.0 to 2.0 to secure estimates of 41^{o} to 65^{o} for glide angle and 6 to 12 m/sec for sinking speed of the bird and ascent rate of the air. Such rates are implausibly high. The birds may have been circling in rotating masses of air, so the forward air speed was substantially higher than the ground speed observed.

Circle durations observed in the Paracas area tended to be longer than those observed in the Cerro Illescas; deflection currents in Paracas are probably more extensive laterally than are the thermal currents in the Cerro Illescas, so Paracas birds were able to follow longer paths in each circle. However, condors circled less frequently in Paracas than in the Cerro Illescas, a contrast apparently due in part to turbulence and a limited extent of vertical movement by deflection currents.

Circle durations lengthened for condors higher above the ground. For 67 observations in the Cerro Illescas, the regression coefficient described an increase of 0.5 second in circle duration per 100 m altitude above the ground, whereas in Colombia, the coefficient for six observations was 5 seconds/100 m. The significant difference between coefficients indicates that ascending air masses increased either in size or rate of ascent more rapidly in the Colombia area than they did in the Cerro Illescas. Estimates of reduced sinking speed due to flapping while circling provide evidence that, for observed flapping rates, sinking speed is only marginally affected. Flapping in this context seems useful only when the difference between ascent rate of the air and sinking speed of the bird is narrow (0.1 to 0.2 m/sec). Condors ascending near broad

canyon walls often did so in elongated, figure-eight patterns. In such a setting, this maneuver may be more useful than a circular one by providing prolonged exposure to a band of rising air with an overall reduction in the banking angle.

Rapid turns are executed by dipping the manus on the side of the turn and rotating the tail, so that the dorsal surface is directed away from the turn. Gradual turns in still air are performed by the tail rotation along. Apparently, the tail acts as an airfoil; rotating the upper surface away from the direction of the intended turn generates a lateral lift component that yaws the posterior of the condor to the opposite side. Occasionally, condors turn by flexing one wing, by arching it, or by turning the head to one side. At times, condors may alter the angles of incidence of the two wings differently to produce steering moments.

The manus of both wings are dipped simultaneously in the double-dip, a maneuver that apparently functions to provide a rapid means of accelerating or changing the angle of attack. The double-dip seems associated with situations where air conditions are changing, updrafts are present, and descending flight paths are sought. Arching both wings simultaneously also precedes accelerated rates of descent and may operate by amplifying the induced drag force.

Condors flying in crosswinds orient the long axis of their bodies upwind from the flight path relative to the ground. Observed angles of heading by 47 condors crossing Playa Chucho resembled expected values calculated with data on velocity of the wind and the condor relative to the ground. In the presence of strong vertical currents, condors frequently glided with feet lowered from the usual location beneath the tail; the lowered feet apparently acted as airbrakes and retarded forward speed.

Patterns of take off and landing varied according to the extent and slope of the perch site. Landing approaches to small perches like cliff ledges involved steep descents similar to those used by pilots for landing on small airfields. A more vertical approach places the bird or airplane

nearer the landing target at a given altitude, so corrections in the flight can be made more accurately. In general, the number of wingbeats in take off increases as the slope of the take off site approaches horizontal.

The flight of immature condors seemed less stable than that of adults. Differences in wing profile in young and mature birds may help offset part of the instability associated with inexperience. Considering spanwise sections with maximum chord length, I computed a stalling speed of 7.3 m/sec for an adult section 47 cm in length, compared to 6.6 m/sec for a section from the wing of an immature bird 52 cm in length.

In Colombia, condors foraged by alternating circling ascents near steep slopes with descending flex-glides over flat areas. Although routes were regular, they were not as fixed as those in Paracas, where flight paths of the condor were restricted to cliff-deflected updrafts of a strong and regular south wind. Condors of the Cerro Illescas region wandered over large areas in flight that was usually powered by thermal updrafts alone.

CHAPTER 9 MORTALITY

This short chapter deals with condor mortality and afflictions. First, I look at parasites, then injuries and sicknesses, and finally, human influences. In the last part, I offer recommendations for the conservation of the condor in Peru and Colombia.

PARASITES

External parasites were collected from an adult male condor shot on Morrow Quemado, Peru, on 22 January 1970, by the wardens of Isla Santa Rosa and given to Dr. Lutz J. Bayer who preserved them and arranged for their identification. A Hippoboscid fly found on the bird was identified as *Olfersia bisulcata* (MacQuart) by Dr. Kenneth MacArthur, and two Mallophaga were identified by Dr. Roger D. Price as *Colpocephalum trichosum*. This species of bird louse has been found only on the Andean condor, whereas the fly has also been collected from black, turkey, and king vultures over an area extending from Texas to Bolivia. From the blind at the nest of pair 2, I saw Hippoboscid flies on the heads of both parents; apparently, the flies were biting them there. Sometimes when the wind ruffled secondary wing and back feathers, as many as five or six Hippoboscid flies were visible at once, moving up exposed feathers toward the skin.

I searched for but found no macroscopic parasites in the digestive tract of the adult male shot on Morro Quemado. An adult male condor that died in captivity at Patuxent Wildlife Research Center after capture in Argentina bore one large nematode in the proventriculus (Locke, *et al*, 1969).

INJURIES AND SICKNESS

Injuries observed most often involved the leg or foot. In Colombia, I saw an immature

male limping for about one week. Nestling 2 limped badly for three weeks after I captured him; apparently muscles has been strained—all bones were intact. An immature male once flew over Playa Chucho with one foot hanging almost 30^{o} below horizontal; he held the other one in the normal position under the tail. On separate occasions, we watched an adult female and an adult male limp on Isla Zárate. When the female flew, one foot hung down. In all of the instances described above, the injury was apparent only by the behavior of the bird; we could see nothing unusual about the legs or feet. In several other instances, however, damage to legs or feet was physically apparent. One adult female that landed and fed on Playa Chucho, Peru had no left tarsus and foot. The joint between the crus and tarsus of one immature female that fed on Isla Zárate jutted out laterally. She landed on the good leg and limped badly when she walked. Once she jumped at several turkey vultures and fell forward on her breast. She spent about 75 percent of her time on the island in sitting or lying positions. Sometimes she held food down with the injured leg while feeding. Twice, I saw her supplant another immature female condor.

Some of the injuries may have occurred when the birds were shot. I found two different sizes of shot encysted in the neck at the base of the head of an adult male condor killed by a warden of Isla Santa Rosa; apparently, the bird had been hit on at least three separate occasions before dying. One ulna of an adult male found dead on a Paracas beach had been broken at the distal end and healed again, with new bone filling a gap about 8 mm wide. The fracture may have been caused by gunshot. During one three week period, AM1 appeared at baits on Colombia with his neck swollen on the back and left side, so that it was almost twice the normal diameter. Several small scabs in the center of the swelling looked like wounds that shot would have left; fighting with other condors could also have caused the injury. Fighting may have been responsible for the mass of scar tissue that partly circled one eye of an immature female visiting a bait in the Paracas area.

Broken flight feathers appeared infrequently. Several condors were observed flying in Colombia and Peru, each with one primary feather on the manus bent directly upwards.

An adult male condor used in a condor-bull fiesta and taken to a zoo in Lima, Peru died shortly thereafter. In an autopsy, cause of death was diagnosed as pneumonia. Undoubtedly, the bird had been weakened by the fiesta experience. Examination of an adult male condor that died in captivity at the Patuxent Wildlife Research Center revealed a relatively high concentration of lead in the liver (38 ppm) and extensive lesions of aspergillosis in the lungs; the primary cause of death was attributed to lead poisoning from ingesting lead shot in food items (Locke, *et al*, 1969).

HUMAN-CAUSED

Pesticides

Pesticides may represent the most insidious and immediately dangerous threat to the Andean condor. A condor shot on the Peruvian coast near Paracas in January 1970 provided fat samples found to contain 320 ppm DDE and 370 ppm PCB, lipid weight (Risebrough *et al*, 1978). Such exceptional concentrations of DDE, the principal metabolite of DDT, likely affect reproduction. High levels of DDE in the tissues of the California condor are associated with eggshell thinning to the extent that this species appears to be, "among the most sensitive of birds to DDE-induced eggshell thinning discovered to date" (Kiff *et al*, 1979). A linear regression of that correlation indicated a 20 percent thinning for approximately 100 ppm DDE. In general, a level of 20 percent thinning has been associated with reproductive failure of other bird species (Hickey and Anderson, 1968; Lincer, 1975).

The peculiar age ratios observed for condors in the Paracas area might reflect reproductive failure of some Peruvian condor populations. In more than 900 observations made

over an 11 month period, only seven percent of the birds observed were immature (Table 67), compared to 43 percent for the population in the Colombia study area (six of 14 birds). Another more hopeful possibility for explaining the Peruvian data is that difficult conditions for flight over the desert barrier between Paracas and distant nesting areas may selectively filter out the younger, more inexperienced flyers. A survey of age ratios in condor populations of the most proximate nesting areas would yield important evidence for this question.

Anomalies in the reproductive behavior of birds may be pesticide-induced. The remarkably extended period of courtship and breeding by one Colombian pair may have been influenced by pesticides. Courtship by this pair occurred over a minimum period of almost four months; copulation postures were observed over a period of at least one month, and possibly four, yet we saw no sign of egg incubation for at least three months following the confirmed observations. In several species of birds, abnormal nesting behavior has been attributed to pesticides, in one instance specifically to dieldrin (Winn, 1973). Herring gull parents, possibly affected by pollutants, neither defended their nests nor were attentive enough at incubation to avoid a high incidence of lethal chilling (Fox *et al*, 1978). Although it is quite possible that condors engage in sexual activities over extended periods, perhaps year around, to cement permanent or semi-permanent pair bonds, the effects of pesticides on reproductive behavior cannot be dismissed without further investigation.

Commercial Hunting

Condors are still considered sacred by many of the desert and mountain people in Peru. Parts of the body like feathers, bones, the heart, stomach, and eyes are used to heal certain ailments. The skin of one adult male condor sold in an Ica market for the equivalent of 25 U.S. dollars (Plate 7). In Nazca, the skin of a condor breast could be purchased for 9 U.S. dollars, and flight feathers were priced at about 30 U.S. cents each. These are 1970 values.

Some condors were trapped alive to be sold to zoos. I saw one Ecuadorian price list offering live condors for 200 U.S. dollars each. J. Schnell and J. Fowler (pers. comm.) met a group of commercial condor trappers in the southern part of the Paracas study area during their work in 1968; the trappers claimed that a Lima dealer wanted 250 condors, but Schnell felt that the large size of the order was only an incentive to encourage the capture of as many birds as possible.

Chapman (1917b) reported an extraordinary number of condors killed near Mendoza, Argentina and sold to Parisian millionaires. One hunter claimed to have killed 16,000 condors, an unlikely number considering the limited extent of the area that the man hunted. More credible are the hunter's reports of shooting a record 114 condors in one day and trapping 61 other birds at one time in a net that circled a dead horse. The hunter presented Chapman with a photograph in which some of the condors are visible in the net trap. The hunter received 10 to 20 dollars for the 84 wing and tail feathers of each bird.

Sport Hunting

Condors are often shot when they allow humans to approach within shooting distance or when the flying birds themselves approach humans. In the Cerro Illescas, condors sometimes landed within 100 m of us, close enough to be shot easily. At the nest of pair 2 in Colombia, both parents perched within shooting distance when we approached the nest. I saw two men approach to within 30 m of IM2 and IM3 when the condors were perched in the Rio Pasto canyon near a trail. In the Paracas area, when I shouted and waved at an adult male and adult female that glided by me, they quickly turned away to one side but then returned and circled within 30 m again. At the Paracas roosts, I could approach perched condors if I made no sharp movements. Whenever hunters and condors were in such close proximity, the hunters usually shot at the birds. A deer hunter in Colombia and a tinamou hunter in Peru both told me that they

had killed condors when this happened. In Colombia, I saw three boys aim their guns at condors gliding above them, but I was too far away to tell if the guns were fired.

Predator Control

A few people who owned livestock in Colombia hunted condors to protect young animals; they claimed that condors sometimes killed them, usually just after birth. To protect newborn goats, a herder in the Cerro Illescas said that he had shot more than 40 condors there in the last 39 years. According to the Peruvian goatherd and several Colombian peasants, leashes tied around the necks of young animals protected them from condors; they said that the wary birds suspected a trap and left them alone.

Servicio Nacional de Fertilizantes

Bird excrement or *guano* is mined for fertilizer on some coastal points and offshore islands of Peru. To encourage better nesting success by the *guano* birds, wardens have been systematically hunting natural predators like the condor and gull for over 50 years. During our period of study, wardens killed condors regularly in three *guana* sites. They shot two or three condors annually both on Isla de la Vieja and on Punta Lomas, a coastal point in southern Peru, whereas the wardens of Isla Santa Rosa took larger numbers (see Figure 4 for a map of the area). Annually, from December to February, the wardens of Santa Rosa traveled to Morro Quemado, a nearby part of isolated coast where sea lions mate and give birth. They shot up to 20 sea lions and then returned to the island. After one or two days, they again visited the mainland and shot condors that had congregated around the dead sea lions. Allegedly, some 50 condor heads are collected annually in this way. We accompanied these wardens on one of their hunts and saw them shoot at and hit nine condors. One adult male fell into the sea and disappeared, and another adult male fell onto the desert. The others flew away wounded. Many more condors have probably died than the number of heads indicated.

We counted the heads of 46 condors reportedly shot by the wardens during the summer of 1968-69 on the island of Santa Rosa. The heads of adult males comprised 70 percent of those taken, whereas immature birds represented only 15 percent (Table 80). Members of one sex and age class were not shot preferentially by the wardens nor were heads selectively taken. The ratio of adult to immature birds approximated that observed on the coast, whereas the ratios for sex varied (see p. 241). We saw males and females in the Paracas study area at about equivalent frequencies. Perhaps the high percentage of males collected can be attributed to the sexual difference in the response toward humans; adult males in flight tended to scrutinize humans more often than females (Table 39). For other kills recorded in South America, the numbers of males and females were nearly equal (Table 80); a majority of these birds may have been taken in nest areas, regions where adults of both sexes might respond similarly to human disturbance.

It is unlikely that the Peruvian population of condors can withstand such heavy losses. Although the great number of birds taken is itself a major threat, the proportion of adults in the kill compounds the effect tremendously. In a demography study of *Gymnogyps,* Mertz (1971) found that the survival rate of immature birds is much less important than adult survival if the population is to remain stable. Assuming pre-adult survival at 50 percent, he calculated adult survival must average at least 86 percent, or the population will decline. This sensitive response to mortality, he points out, demonstrates why the *Gymnogyps* populations were so quickly decimated with the advent of firearms.

A decline in the number of condors on the Peruvian coast in the last 25 years had been noted by wardens of both Isla Santa Rosa and Isla de la Vieja. Two or three condors had been seen and shot annually on Isla de la Vieja in recent times; in 1947, 30 condors were slain there in two days. Persecution by bird island wardens is probably responsible for the apparent decline.

The decimation of coastal condors by wardens of Isla Santa Rosa is not warranted.

Table 80. Condor mortality and capture recorded from 1968 to 1970. About 95 percent of the birds listed were observed personally or were verified by photographs; fate of the remaining birds was confirmed by more than one source.

	Condors captured				Condors killed					
	Adult		Immature		Adult			Immature		
	Male	Female	Male	Female	Male	Female	Unknown	Male	Female	Unknown
Control by guano-bird wardens					36	7		7	7	2
Dead, on display[a]					5	5	1			
Live, captive	9	9	5	4	2	3		2	2	
Killed in the *condor-rachi*					1			1	2	
Captured for condor-bull fiestas	2		3	2						
Others					1	1		3		1
Total - Paracas area	2	2	0	0	38	11	0	4	13	0
Total - South American locations other than Paracas	9	7	8	6	7	5	1	9	8	3
Total	11	9	8	6	45	16	1	13	11	3

[a] I have assumed that condors on display were killed by collectors. A small fraction may have been of birds that died in captivity.

During our visit to the island, over 50 condors fed on sea lions only several kilometers away, yet not one of them flew to the island. Condors had not been seen on Isla Santa Rosa for seven years when we were there in January 1970. The heavy persecution of condors in that small area may well have been responsible for a general decline in the number of condors over all of the Peruvian range. Fortunately, in November 1970, the government banned condor control by the Servicio Nacional de Fertilizantes. The ban is part of a general resolution that prohibits any killing or capture of condors except for scientific purposes.

Use in Traditional Fiestas

The Condor-Bull Fiesta

Condors are used in condor-bull fiestas in a number of mountain villages of southern Peru (see p. 30). In 1969, these fiestas were held in Cuzco, Cotabambas, Grau, and Tambobamba. In Pampachiri, Larcay, Zorras, Pampas, Campaña Hacienda and Chumbibilcas, the fiestas may have occurred as they have in the past. There were no condor-bull fiestas in Paruro, Lucanas, Andahuaylas, and Puquio in 1969, but they have been held there in former years. This celebration is held on various dates depending on the village; many are held on national or religious holidays such as July 28, September 8, or December 8.

We observed two fiestas (see Plates 9,10, 36). Of the three condors used in these celebrations, two probably died as a result of injuries. Although the condors are cared for, little can be done if a condor is entangled in the ropes used to release or recapture the bull. Frequently, the condor is crushed between the fence and the bull. We saw one bull crash through a doorway and into a house beating the condor against the walls. In some villages on the highland plateaus, where wood is scarce, the bulls break through the weak fences; several condors reportedly died with the bulls when the animals rushed over the edge of a nearby canyon.

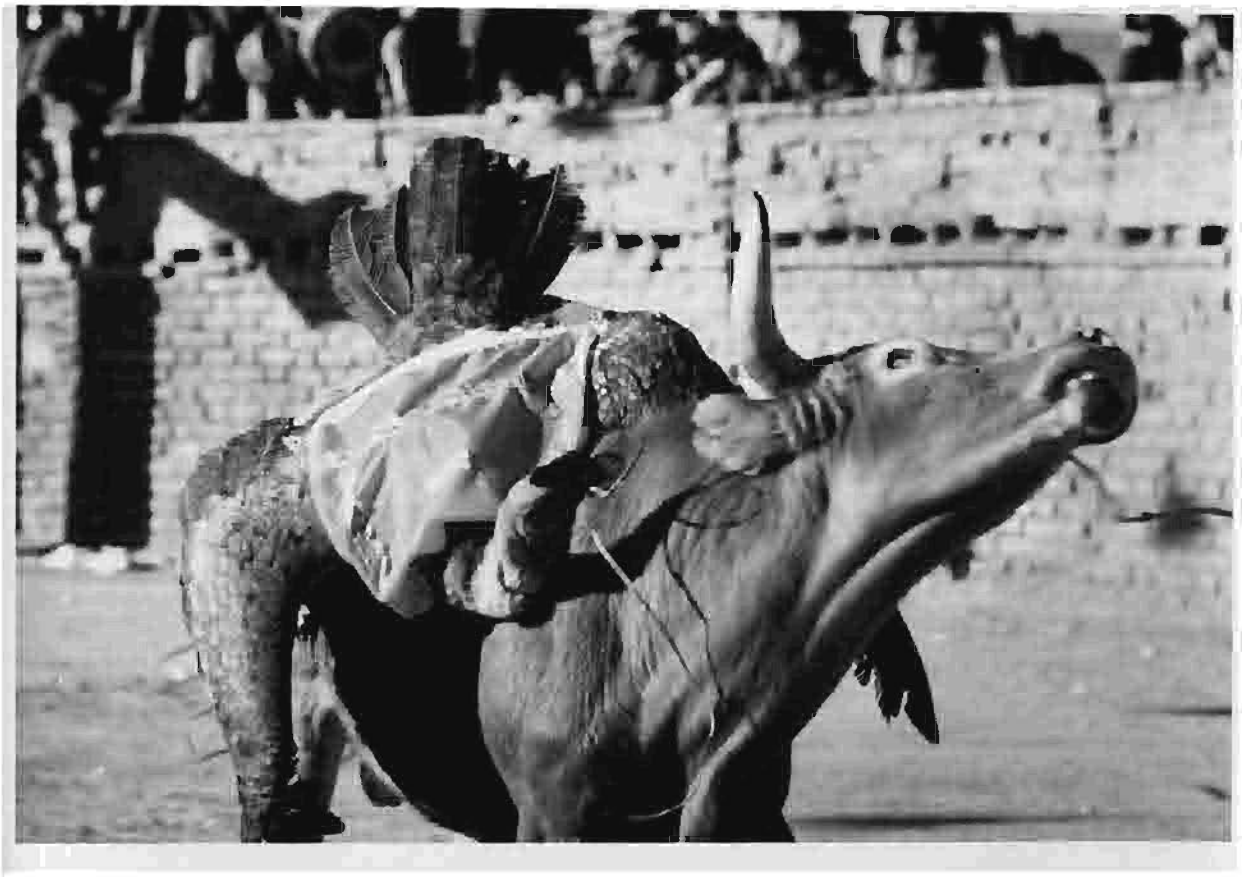


Plate 36. A condor-bull fiesta in Cuzco, Peru in 1969.

Condors may die after they have flown from their release site. One bird that we observed at the celebrations was very young and may still have been dependent on parental care after leaving the nest. Even if released in good health, a bird of that age would probably die. At least a third of the condors used in the condor-bull fiesta probably perish. According to one reliable villager I interviewed in the Cuzco area, six of 12 condors used for one fiesta in the Larcay region died before their release.

The Condor-rachi

During *carnavales,* held in the second week of February, around 10 to 15 condors were destroyed each year in the Callejon de Huaylas region of northern Peru (Plates 11, 12). The *condor-rachi* or *arranque del condor* is a fiesta centered around the ritual beating of a condor tied and suspended from a rope (see p. 32). When we were in Peru, the following villages practiced the *rachi* when they could secure condors: Huata, Quespa, Cullashpampa, Huino, Campiña, Santa Cruz, Wankawasi, Cochamarca, and Cashapampa. Condors were killed in other more isolated villages. In several fiestas, two condors were destroyed at one time.

Every condor trapped for use in the ritual dies. Some condors die before the fiesta. In 1969 at Cullashpampa, one condor died from an overdose of alcohol. In most festivals, the birds are given alcoholic chicha, or corn beer, to drink. 1970, near Campiña, a condor died from mistreatment during the journey from the trapping site. In 1970, we saw six condors that had been trapped for the *rachi*, and we watched two of them die in the fiesta, one at Cullashpampa and the other at Cashapampa (Table 80).

The *rachi* was once held in the larger towns of Caraz and Yungay. They have since been prohibited because of the brutality. In 1970, the *rachi* was prohibited for that year in Huata and Quespa, because it was believed the condors might spread foot-and-mouth disease prevalent among livestock of that region at the time. In most of the other Peruvian villages of this region,

the *carnaval* celebrations are centered around the *corta-monte*, a ritual in which a tree is slowly chopped down. This more humane practice should be substituted for the *condor-rachi*.

Methods of Capture

A group of Indians trapped the condors we saw in the condor-bull fiestas on the *puna* or high altitude plain. They left a dead horse in a depression, and the trappers lay hidden around it. When the condor arrived and began to feed, the men rushed out together from all sides, throwing *ponchos* and *bolos* to entangle the startled bird. Condors taken for the *condor-rachi* in northern Peru were lured to a dead sheep lying atop a brush-covered pit where two men sat waiting. When a condor landed, one trapper reached up through a hole in the brush frame and grabbed a leg of the bird, and the other tied it down.

A few other methods of capture have been described (Apolinar, 1914, Castellanos, 1923, Housse, 1940). They reported some condors were caught after being anesthetized by vegetable substances placed inside baits. Others were taken after alighting beside trappers covered with the skin of a cow or horse. Several people claimed that they had captured condors after luring them to baits inside fences or steep gullies; reportedly, the food-laden birds could not take off when surprised by the hunters. Darwin (1845, see p. 5) describes this method and another where condors are taken from the roosts at night.

CONSERVATION OF THE CONDOR IN PERU AND COLOMBIA

Although both Peru and Colombia provide legal protection for the condor, little has been done to enforce these laws. Even though the first stage in management to conserve the condor is to limit the destruction of the birds themselves, another equally important stage is the establishment of reserves where the birds can feed and nest in safety. Appreciation for the bird and its protection should be the goal of an educational program.

Mertz (1971), in his demography study of *Gymnogyps*, reasoned that adult survival has a much greater effect on the population than pre-adult survival. He pointed out that the sensitivity of nesting adults to disturbance, which would have been adaptive in earlier times, may now be a handicap if birds exposed to innocent human activities abandon their nests. Nesting areas protected from human disturbance are a likely prerequisite for viable populations of the Andean condor as well. The rapid encroachment of man into the few remaining wildernesses of Peru, Ecuador, and Colombia threatens the existence of the species in those countries. Condors disappeared from Venezuela at the turn of the century (W. H. Phelps, Jr., pers. comm.) and may soon disappear from Colombia.

The three areas used for study in this research program were excellent locations for condor reserves. Although the Colombia study area is no longer inhabited by condors, both locations in Peru remain important sites.

In the Paracas study area, Punta Zárate would be an excellent observation point for visitors. In the summer, tourists with an interest in archeology and sport fishing could also be assured of seeing condors feeding on Isla Zárate amid the harems of sea lions gathered there. From the end of Punta Zárate, observers would often get spectacular views of condors as the birds fly over the point, on their way to and from the island. A warden should be on duty here at all times to prevent abuses. He should be supplied with a spotting scope to help visitors view the condors as they feed and move about the island. The Paracas Peninsula and nearby Morro Quemado areas would be excellent sanctuaries for both condors and sea lions. Except for travel by boat and observation from the sea, people should be prohibited from entering and disturbing these areas. The Paracas Peninsula has been a National Reserve since 1975, a designation that calls for the rational management of all resources there.

The Cerro Illescas range is also an optimal location for a sanctuary. Except for a single

goatherd living on the southern end of this 600 square kilometer range, these mountains were not inhabited by humans when we were there. Fishermen do not frequent the beaches on the coast west of the range. Here, undisturbed, condors roost and probably nest in the mountains, feed on the isolated beaches, and maintain flight routes independent of human activities. A good road crosses from Sechura to a phosphate mine at Bayovar on the edge of the range. Here condors can be viewed daily. Travel within the range would be unnecessary and should be prohibited.

CHAPTER 10 CLOSING PERSPECTIVES

To conclude this biological inquiry of the Andean condor in nature, the following section reviews briefly the major points covered in the study, considers the current status of the species, and suggests further research needs. The chronology of subjects corresponds to the chapters.

SUMMARY OF MAJOR POINTS

The comparatively phlegmatic condor regularly spends hours perched in the nest, roost, or feeding areas, so much is revealed in its attendance to body care and its sensitivity to the changing weather. Details of the mechanics and content of each movement can aid in determining taxonomic affinities with vultures and other birds and in clarifying the purpose of these behavior patterns. The ethogram itself has been presented here as reference material for other comparative research. Results in the examination of function were neither startling nor strongly conclusive. For example, stretching may be a "warm-up" for activity; preening may serve a communication role along with that of feather maintenance; body shaking likely functions in feather arrangement. In the investigation of weather-related effects, however, condors revealed the most surprisingly distinct responses: Perch selection and posture are clearly related to the presence of the sun; the onset and level of foraging activity are intimately related to the degree of air movement; panting, raising the ruff, and the methodical application from one tarsus to the other of white excretory material are patterns clearly related to the difference in ambient and body temperature. Although other birds may be as sensitive to weather conditions, their more active habits offers less for the wingless human to follow and witness.

The extended periods of observation revealed much about the nature of pair bonds for

several identified pairs of condors. The most prominent expression of sexual activity observed was the spread-wing courtship posture, a stance employed more frequently by the male but with more animation and for longer durations by the female. The activity was usually a midday occurrence. Courtship might indicate a level of physiological readiness, a swifter, more intense state for the female when the production of a single egg requires fertilization within a certain period. Copulation was preceded by courtship with the posture assumed by the bird mounting. Peculiarly, mates of either sex were observed mounting. Sexual activity beyond the apparent and immediate function of reproduction presented another unusual aspect of Andean condor behavior: Courtship occurred regularly throughout the last nesting phase of one pair; marked sexual activity characterized the relationships of one pair, even though they did not nest during a four month period of close observation. Sexual activity was common among the Paracas gatherings of transient adults. Such activity may act to cement permanent or semi-permanent pair bonds. We found associations and sexual interactions with stronger expressions between nonnesting mates than between nesting birds; attendance to the young may substitute for an attendance to one another in maintaining the pair bond. The shelter of male dominance in feeding groups would provide a distinct advantage to a female mate, a mutual advantage when the year-round health of the pair furthers the chances of successful reproduction.

As with most vultures of the world, gatherings at roosts or at food are common events. These birds lend themselves particularly well to the analyses of social behavior. Except for flight, no other aspect of vulture life is apt to contribute as much to our overall understanding of bird biology as group relations, nor is any other vulture as well suited for this examination as the Andean condor, where a marked distinction of sex and age allows the investigator four large categories or "teams" in which he can search out characteristic strategies.

The simplest and clearest features of the condor social organization included: a general

dominance by males over females and by adults over immature birds, a characteristic aggressiveness in male-male relationships, negative associations among adults of the same sex, and positive ones for young birds. Interactions among birds of a resident population were found to be smoother, quicker, and less aggressive than those of transient gatherings. Overt aggressiveness apparently served as a test of dominance and occurred rarely among birds of separate sex-and-age classes, where dominance had clear expression. A linear and unidirectional dominance hierarchy occurred within as well as across different sex and age classes, not only in resident populations, but among transient groups as well. Possibly, these transient populations moved as blocs, retaining many specific individuals known to one another.

If this "clanning" was unique to the Andean condor among the Cathartidae, it might explain the anomaly of sexual dimorphism for this species, in particular the distinct individuality of the head and crest of adult males, the dominant class. Across the span of evolutionary time, the individual composition of other cathartid populations might have been characteristically more fluid and ephemeral in nature. If so, the degree of recognition in perceiving certain classes and individuals necessary for establishing a functioning linear hierarchy would not have been the adaptation that it was for the Andean condor. In such a system, dominance grants priority of access to one bird at a minimum of expense to both potential contestants when the hierarchy reflects the actual likelihood of winning a struggle for whatever resource is contested.

Territoriality, a locality-related effect that can supersede patterns of dominance established in other contexts, also figured in condor relations. One nesting pair had exclusive use of certain perches, a roost, and a bathing and drinking area on a single cliff frequented by two pairs, even though the nesting male was subordinate at food to the male of the other pair. In areas away from the nest, condors often congregated at communal roosts and day perches. Dominance in Andean condors is linked to wariness at food; dominant birds, with their wider

range of choice in the time and place of feeding, seemed more sensitive to dangers outside of the condor society.

In the analysis of feeding behavior, I found that mammals comprised nearly 80 percent of the diet in one area, even though birds were preferred. Feeding sites selected on large animals were related in part to the sex of the condor, with larger males most often tearing the skin and feeding in newly opened areas. In the Paracas area, turkey vultures were comparatively generalist feeders, taking more equal portions of birds, human refuse, and other items. Compared to condors, the smaller vultures preferred feeding just after dawn, whereas condors fed more often at midmorning, a difference related, no doubt, to variations in their dependency on wind for flight. Parallel with this tendency to a more generalized diet and a wider range of possible feeding time, turkey vultures were able to feed with greater impunity near human settlements and activities. These additional restrictions placed on condors may force them to undergo seasonal movements of larger scale than their smaller cousins, even though the larger vultures with their lower rate of metabolism can probably withstand longer periods without food. As a group, New world vultures are relatively generalist in nature compared to the Old World vultures in Africa. Greater supplies of available food and more ideal and extensive conditions for large-scale flight in Africa were probable factors in the evolution of more species and higher specialization in the Old World group.

Nervousness exhibited by condors of all sex and age classes seemed important in avoiding humans. Adult condors were more alert than immature birds. On the Peruvian coast, condors did not feed on open and exposed beaches until forced there by a shortage of food (39 percent of the population was supported on beaches when the amount consumed per bird fell to 200 g; when the amount consumed reached its peak at 600 g/bird, only 0-3 percent of the condors supported themselves there). As an approximate average, the beach stratum supported

only one of five condors living on the coast, one of eight to 20 turkey vultures, and one of 500 gulls. Most of the vultures fed at the base of sea cliffs or on islands, whereas the gulls usually fed from the water

The large size, relatively slow wing and body movements, and predictable flight paths of the condor offered exceptional conditions for the study of aerodynamics and permitted a derivation of values for air speed, lift coefficient, induced drag, and glide ratio. Using these exponents of equilibrium gliding flight, an analysis of slow-motion cine film generated a rough picture of the changing direction and speed of air around the moving wing and allowed several major conclusions: First, flapping acts to produce lift and propulsion in take off; in level flight, it furnishes only lift and even slightly retards forward motion. Second, lift and propulsion can be produced in either the up- or downstroke, but the anterior advancement of the downstroke axis ensures that maximum lift forces are produced during the wingbeat phase of optimal mechanical efficiency. Evidence from both observations of behavior and from an analysis of power output indicates that condors are incapable of sustained flight in still air and must rely on updrafts to fly. That dependence is apparent in the discrete modes of flight used for different areas: Circling flight patterns were rare in the Paracas area but covered relatively large distances in these laterally extensive but turbulent updrafts; figure-8 patterns were often employed during early flights in Colombia, a configuration that permitted more exposure to a narrower band of rising air without the steady drain of an inefficient banking angle. Circling patterns infer that thermal currents rise faster or increase in size more rapidly in Colombia than in the Cerro Illescas. Analysis of the profile changes in different flight patterns or among birds of different ages allowed a number of generalizations on the function and mechanics for patterns of steering, for methods or recovering stability, gaining or losing speed, and maintaining a proper trim.

CURRENT STATUS AND RESEARCH NEEDS

In Colombia, the Andean condor has left the Rio Pasto and Rio Juanambu canyons, the area where we worked. A new highway, a section of the Pan-American, bisects the area; it is unlikely that the big vultures will ever return to this place that was once, by virtue of its inaccessibility, a domicile and refuge. In Ecuador, condors are legally protected, but practical enforcement of the law is carried out in only five protected Natural Areas. According to Carlos Aguirre C., Director General Desarrollo Forestal (letter dated October 1970), Ecuadorian condors have been decimated by massive applications of cyanide poison. In areas where gatherings of 30 to 60 condors were seen 40 years ago, groups observed now are comprised of only five to eight birds at most, usually one to three. He lists the principal concentrations of remaining condors in Ecuador as follows: the Chiles Mountains in the province of Carchi, the Cayambe range in the province of Pinchincha, the Run-tún in Tungurahua, the Chimborazo and Cubillín in the province of Chimborazo, and parts of the Yangana, Nambacola, and foothills of the Zamora in Loja.

Since we left Peru, a number of legal measures brighten prospects for the bird's preservation there. (1) The hunting or capture of condors, except those taken for scientific purposes is prohibited; this law (Resolución Ministerial No. 5056-70-AG of 30 November 1970) precludes any form of condor control in the management of *guano* birds. (2) As one provision of the same law, condor-bull fiestas are illegal and under penalty of heavy fines. (3) An area of 335,000 hectares, including the Paracas Peninsula, was established in 1975 as a National Reserve of Paracas (Decreto Supremo No. 1281-75-AG).

The condor-rachi festival of northern Peru has become less of a threat in the last decade. According to Carlos Ponce, Director of Dirreción de Conservación (Dirreción General Forestal y de Fauna) the festival, if it is practiced at all, occurs only in a few of the most isolated areas,

owing to a publicity campaign against it, and to a massive exodus of people from that area following the great earthquake of 1970. Although these developments and measures afford some optimism in the future of the bird, effective enforcement of legal measures remains the greatest challenge, not only in Peru, but in all Andean republics where the focus of both attention and funds is concentrated in areas of more immediate economic concern.

In the United States, the Andean condor is recognized as an endangered species by the government. As required by the Endangered Species Act of 1973, the U.S. maintains a list of endangered and threatened species, in categories both domestic and foreign. *Vultur* is also listed with CITES, the Convention on International Trade in Endangered Species of Wild Fauna and Flora, where the condor is included in Appendix 1, a division advising the strictest control measures in international trade. The Red Data Book, an appraisal of endangered species on a world-wide basis compiled by the International Council for Bird Preservation, does not yet list *Vultur*. Warren King, compiler of the book advised me that although the bird is seriously endangered in the northern part of its range, the status of the species is vague for the southern two-thirds of its range (from Bolivia south). If an examination of the species in that area bears evidence of any decline, a future revision of the Red Data Book will include the species.

For the North American counterpart, *Gymnogyps*, the status is not as vaguely known nor are the latitudes of management error anywhere comparable. The total population probably embraces fewer than 50 individuals (Wilbur, 1976, 1978). Recent trends have been discouraging; according to Wilbur (1978), the number of fledglings for the entire population average only 1.5 per year between 1968 and 1975 with no more than two fledged any single year. Emergency plans by the U.S. Fish and Wildlife Service to stem the decline and eventual extinction of *Gymnogyps* included a program of habitat protection; capture, marking, and radio tracking, and captive propagation. Finally, amid much controversy, a decision was made to trap

every wild-living California condor with the hope of raising and eventually reintroducing young birds; in April 1987, they caught the last wild condor in California.

Pilot studies for the propagation work employed captive Andean condors. These birds have laid a total of 21 eggs, all of which hatched. Eight were raised to flight age. In cooperation with the project, the Bronx Zoo has reared five young birds (U.S. Fish and Wildlife Service, 1979).

In view of the success that zoos, most notably the San Diego Zoo, have had in raising condors, the major difficulty in captive propagation programs would not seem to be in raising the birds but in releasing them. Devising an effective substitute for parents of dependent juveniles presents a major challenge. To trouble-shoot these problems, groups of young transmitter-equipped Andean condors raised at Patuxent and the Bronx Zoo were released in the Cerro Illescas area (S. Temple and M. Wallace, University of Wisconsin, pers. comm.). By the fall of 1993, 71 California condors remain in captivity in the Los Angeles Zoo and the San Diego Wild Animal Park. Five of eight one- to two-year old young that have been released still survive, but the young, incautious wanderers have been vulnerable to powerlines and other human-related dangers.

Further research on *Vultur* dealing with conservation and scientific problems of that species should begin with an examination for the possible effects of pesticides. To determine if pesticides are responsible for the skewed age ratios observed in the Paracas area, nearest nesting areas should be canvassed to secure estimates of age ratios there. If the preponderance of adults on the coast is due to the difficult flight conditions between that area and nesting regions, the age ratios should be markedly different, particularly when condors are frequenting the coast. A collection of additional fat samples from these and other areas are of special importance. A car-survey of accessible valleys in Peru, Bolivia, Argentina, and Chile should be undertaken to

determine rough estimates of the bird's prevalence, with data recorded on the sex and age ratios and crop contents (to aid in evaluating the habitat) of birds observed. Interviewing observant resident people for clues on population trends of the species would help in gauging recent changes.

Detailed observations of adult behavior during the early phases of nesting in nature are yet to be recorded and are of primary importance not only to bridge a gap in the bird's life history, but also in management practices for periods when any disturbance may be critical. The duration of the breeding cycle in northern and southern climes needs to be determined, as does the extent of juvenile dependency. Several questions presented in this study are of a more purely scientific interest. One hypothesis generated for the expression of sexual dimorphism among Andean condors is that it enhances conditions for individual recognition among males in populations, which compared to those of other vultures, are more stable in composition. Are *Vultur* populations indeed comparatively stable? Additional study of *Vultur* social behavior is likely to bear the greatest fruit in contributing to our understanding of the biology of vultures, of other birds, and other scavengers in general. The species, by virtue of a unique and characteristic sociality and an unusual level of individual differentiation, promises much to any pursuit of the function and evolution of social behavior.

To conclude, then, the Andean condor offers much to the scientist, to the naturalist and casual observer, to the people who live where it lives and to the people that come to see. It is time to guarantee that this creature is not badgered into a dwindling and pitiful existence with all of them marked and transmitting radio signals. The gift of the condor is surprise, when suddenly this, this seeming relic of another time, blesses you with its own curiosity, and passes overhead so near you can hear the pinions whine and see the color of the eye. As programs for the preservation of the California condor use their Andean brothers to sort and void the errors for

hopeful restoration, let us use the tragic example of the northern condor to save us from losing the free-living populations of the southern continent.

FOOTNOTES

Chapter 1

1. Scientific names of animals given in the text are listed in Appendix A.
2. Nearly 5000 miles. 1 km = 0.6 miles; 1 m = 3.2 feet; 1 cm = 0.39 inch; 1 kg = 2.2 lbs.
3. Taken from Barrionuevo (1969).
4. Geology information taken from maps provided by the Comisíon Carta Geologica Nacional.

Chapter 2

1. Parametric statisical tests are from Steel and Torrie (1960), and nonparametric tests are rom Siegel (1956). I did not use Yate's correction factor in chi-square tests, a deletion recomended by Grizzle (1967). Some chi-square tests were performed when expected frequencies were less than five (see Cochran, 1954); in these instances the small expected values are given with the test, or the condition is noted in the text or caption. Raw data are presented in all such instances for the reader who wishes to apply other statistical treatments. Other modifications of statistical tests are described in the sections where they are used.
2. $p<0.05$, median test
3. $X^2=5.03$, $p<0.05$
4. $p<0.002$, Mann-Whitney U test for durations; $X^2=13.09$, $df=3$, $p<0.01$ for the timetables
5. $r=+0.30$, $p<0.05$
6. $p<0.05$, Fisher test
7. 27 runs, $p<0.05$
8. $X^2=17.56$, $p<0.001$

9. Paracas, $p<0.025$, Mann-Whitney U test; Colombia, $p<0.001$, median test

10. $p<0.05$, Mann-Whitney U test

11. $r=-0.15$, $p>0.1$

12. $r=-0.18$, $p>0.1$

13. $r=+0.48$, $p<0.02$

14. $r=+0.48$, $p<0.02$

Chapter 4

1. $p<0.02$, binomial test

2. $X^2=14.20$, $p<0.001$; for other adults, $p<0.1$, Fisher test

3. $X^2=6.53$, $p<0.02$, median test

4. $X^2=20.85$, $p<0.001$

5. $X^2 + 9.92$, $p<0.01$

6. $X^2=6.70$, $p<0.01$, $n=51$, pair 2 not considered in this test

7. $X^2=29.59$, $df=5$, $p<0.001$

8. $X^2=14.18$, $df=10$, $p<0.20$

9. $X^2=11, 35$, $p<0.001$

10. $p<0.05$, Fisher test

11. $p<0.01$, Mann-Whitney U test

12. $p<0.06$ Mann-Whitney U test

13. $p>0.1$, Mann-Whitney U test

14. $p=0.90$, Mann-Whitney U test

15. $r=-0.15$, $n=27$

16. $n=110$, $X^2=16.69$, $df=11$, $p<0.20$

17. X^2=21.21, *df*=10, *p*<0.02

18. X^2=0.38, *df*=1, *p*>0.8

C**hapter 5**

1. *n*=113, X^2=6.10, *df*=6, *p*<0.30

2. X^2=13.37, *df*=1, *p*<0.001

3. Kolmogorov-Smirnov test, D=0.13 when two birds were present; D=0.10 when more than two birds were present

4. *n*=703, X^2=81.30, *df*=18, *p*<0.001

5. *n*=180, X^2=21.19, *df*=10, *p*<0.02

6. *n*=182, X^2=56.97, *df*=16, *p*<0.001

7. *n*=90, X^2=16.59, *df*=8, *p*<0.05

8. *n*=188, X^2=21.04, *df*=6, *p*<0.005

9. X^2=3.69, *p*>0.10

10. *n*=239, X^2=24.66, *df*=10, *p*<0.01

11. *n*=133, X^2=16.61, *df*=8, *p*<0.05

12. *n*=459, X^2=20.22, *df*=7, *p*<0.01

13. *n*=125, X^2=27.72, *df*=5, *p*<0.001

14. *n*=683, X^2=66.19, *df*=9, *p*<0.001

15. X^2=66, X^2=9.61, *df*=4, *p*<0.05

16. *n*=160, X^2=35.08, *df*=6, *p*<0.001

17. *n*=142, X^2=15.76, *df*=5, *p*<0.01

18. *n*=491, X^2=33.75, *df*=9, *p*<0.001

19. *n*=728, X^2=31.74, *df*=9, *p*<0.001

20. n=239, X^2=24.66, df=10, p<0.01

21. n=133, X^2=16.61, df=8, p<0.05

22. peck/jump approach, n=188, X^2=21.04, df=6, p<0.005;

simple approach, n=90, X^2=16.59, df=8, p<0.05

23. n=90, X^2=3.00, df=1

24. n=373, X^2=49.96, df=5, p<0.001

25. n=56, X^2=22.20, df=2, p<0.001

26. n=38, X^2=38.00, df=1, p<0.001

27. n=71, X^2=15.45, df=3, p<0.01

28. n=28, X^2=4.23, df=1, p<0.05

29. n=32, X^2=3.86, df=1, p<0.05

30. t=2.61, p<0.02

31. n=110, X^2=7.57, df=2, p<0.05

32. X^2=9.33, p<0.01

33. n=43, X^2=4.33, df=1, p<0.05

34. Kolmogorov-Smirnov test, D=0.32, p<0.01

35. Kolmogorov-Smirnov test, D=0.21

36. X^2=17.48, p<0.01; one expected value in this test is less than five but exceeds two (see pg. 126)

37. n=66, X^2=22.08, df=4, p<0.001

38. n=40, X^2=7.50, df=2, p<0.05

39. n=68, X^2=12.51, df=2, p<0.01

40. n=77, X^2=37.01, df=6, p<0.001

Chapter 6

1. $p<0.02$, median test

2. $p<0.01$, median test

3. Adult male rates in Colombia>adult male rates in Cerro Illescas, $p<0.1$, median test; adult female rates in Colombia>adult female rates in Cerro Illescas, $p<0.05$, median test.

Chapter 7

1. $n=939$, $X^2=41.10$, $df=12$, $p<0.001$

2. Immature males, $t=8.26$, $p<0.001$; adult females $t=2.84$, $p<0.005$; and immature females $t=7.70$, $p<0.001$

3. Adult female-immature female visitations, $t=5.86$, $p<0.001$, and feeding bouts, $t=2.55$, $p<0.01$; adult male-immature male feeding bouts, $t=4.99$, $p<0.001$

4. $X^2=13.56$, $df=6$, $p<0.005$

5. $n=208$, $X^2=14.46$, $df=2$, $p<0.001$

6. $n=220$, $X^2=0.48$, $df=2$, $p<0.1$

7. Mann-Whitney U test, $p<0.002$

8. $X^2=32.07$, $df=8$, $p<0.001$

9. $X^2=120.10$, $df=12$, $p<0.001$

10. $X^2=33.64$, $df=4$, $p<0.001$

11. $X^2=10.67$, $df=2$, $p<0.01$

12. Sex ratios, $X^2=23.80$, $df=8$, $p<0.01$; age ratios, $X^2=32.87$, $df=8$, $p<0.001$

Chapter 8

1. $p<0.01$, median test

2. Condors, $r=+0.14$; turkey vultures, $r=0.03$

3. $p<0.01$, Mann-Whitney U test

4. $p<0.01$, Fisher test

5. $t=2.04$, $p<0.05$

6. $X^2=9.38$, $p<0.01$

7. $X^2=20.24$, $p<0.001$

8. $X^2=11.48$, $p<0.001$

APPENDIX A

Common and scientific names of wild birds, mammals, reptiles, and fish mentioned in the text.

BIRDS

Order Sphenisciformes

Humboldt penguin	*Spheniscus humboldti*

Order Procellariiformes

fulmar petral	*Fulmarus glacialus*
southern fulmar	*Fulmarus glacialoides*
giant fulmar	*Macronectes giganteus*
Peruvian diving petrel	*Pelecanoides garnotii*

Order Pelecaniformes

brown pelican	*Pelecanus occidentalis*
white pelican	*Pelecanus onocrotalus*
eruvian booby	*Sula variegata*
guanay cormorant	*Phalacrocorax bougainvilli*
red-legged cormorant	*Phalacrocorax gaimardi*

Order Ciconiiformes

Marabou stork	*Leptoptilos crumeniferus*

Order Falconiformes

Andean condor	*Vultur gryphus*
California condor	*Gymnogyps californianus*
king vulture	*Sarcoramphus papa*

black vulture	*Coragyps atratus*
turkey vulture	*Coragyps atratus*
greater yellow-headed vulture	*Cathartes melambrotus*
lesser yellow-headed vulture	*Cahartes burrovianus*
golden eagle	*Aquila chrysaetos*
black-chested buzzard-eagle	*Geranoaetus melanoleucus*
red-backed buzzard	*Buteo polyosoma*
lammergeyer	*Gypaetus barbatus*
European griffon vulture	*Gyps fulvus*
white-backed vulture	*Gyps africanus*
Rüppell's vulture	*Gyps rüppellii*
Cape vulture	*Gyps coprotheres*
hooded vulture	*Necrosyrtes monachus*
white-headed vulture	*Trigonoceps occipitalis*
Egyptian vulture	*Neophron percnopterus*
lappet-faced vulture	*Torgos tracheliotus*
osprey	*Pandion haliaetus*
crested caracara	*Polyorus plancus*

Order Charadriiformes

Peruvian gull	*Larus belcheri*
gray gull	*Larus modestus*
kelp gull	*Larus dominicanus*
herring gull	*Larus argentatus*

Inca tern	*Larosterna inca*
Order Psittaciformes	
Budgerigar	*Melopsittacus undulatus*
Order Apodiformes	
ruby-throated hummingbird	*Archilochus colubris*
Order Passeriformes	
common raven	*Corvus corax*
common grackle	*Quiscalus quiscala*
red-winged blackbird	*Agelaius phoeniceus*
black-capped chickadee	*Parus atricapillus*
mountain chickadee	*Parus gambeli*
titmice	*Parus major*
	P. caeruleus
	P. paluetris
MAMMALS	
coast fox	*Dusicyon griseus*
coyote	*Canis latrans*
Burmeister's porpoise	*Phocaena spinipinnis*
Sea lion	*Otaria flavescens*
fur seal	*Arctocephalus australis*
vicuña	*Vicugna vicugna*
mule deer	*Odocoileus hemionus*

FISH

blue shark	*Prionace glauca*
mullet	*Mugil cephalus*
grunt	*Anisotremus scapularis*

REPTILES

green turtle	*Chelonia mydas*

APPENDIX B

ASSOCIATIONS IN FLIGHT

Associations of adult condors in flight were measured by comparing the number of pairs of adult birds seen together in flight with expected values generated from observations of all class-identified condors observed in flight. Hence, in Colombia during 46 days of observation from 28 June 1968 to 11 November 1968, I recorded 15 instances of one adult male and one adult female flying within 300 m of one another and no instances of either two adult males or adult females. Observations recorded (a) within 5 km of a known nest site and (b) during periods when baits were used were excluded from this analysis. The total number of occasions adult males were seen in flight were 65; for adult females, the figure was 22, and for immature birds, five. Values for immature condors were disregarded in this analysis.

From these individual occurrences, the probability computed that any two adults observed flying in the same area were:

(a)both adult males $\left(\frac{65}{65+22}\right)^2 = 0.06$

(b)both adult females $\left(\frac{22}{65+22}\right)^2 = 0.06$

(c) one adult male and one adult female

$$2\left(\frac{65}{65+22}\right)\left(\frac{22}{65+22}\right) = 0.38$$

Multiplying these probability values by 15, the total number of instances two condors were seen

together in Flight, I obtained expected values of 9.3 for observations of either two adult males or two adult females and 5.7 for the male-female pair. Applying a chi-square test with observed and expected values, I found that significantly more male-female pairs were observed than expected ($X2 = 24.47$, $df = 1$, $p<0.001$).

In a similar treatment of data from Peru, I searched for male-female associations in condors crossing Playa Chucho and the Zárate channel. Data in both instances were recorded on condors traveling the same direction within one min of each other. On Playa Chucho I saw nine pairs of adult males, six adult male-female pairs, and three adult female pairs. The total number of occasions when class-identified condors were observed in flight across Playa Chucho were as follows: adult males, 138; adult females, 115; and immature females, 11. These data were recorded on three days from 11 April 1969 to 15 April 1969 and on 14 days from 28 December 1969 to 11 January 1970. Associations of the pairing according to sex were not significant ($X^2 = 3.57$, $df = 2$, $p<0.20$).

Data at the Zárate channel were recorded from 7 October 1969 to 22 February 1970. Of 35 adult pairs seen, three were both males, six both females; and 26 male-female pairs. The frequency of condors observed in flight either alone or in a group was as follows: 75 adult males, 103 adult females, and three immature females. Associations according to sex were significant with more male-female pairs observed than expected ($X^2 = 9.06$, $df = 2$, $p<0.02$).

APPENDIX C

BLACK AND TURKEY VULTURE SUPPLANTING RELATIONS

I compared an observed frequency of peck/jump approaches in both intraspecific and interspecific supplanting patterns by turkey and black vultures with expected values derived from the number of vulture minutes recorded at the bait. The total number of turkey vulture minutes recorded at the Cerro Illescas baits in this analysis was 810 min and for black vultures, 845 min. Therefore the probability that peck/jump patterns involve each across- and within-species combination is computed as follows:

(a) turkey vultures supplant turkey vultures

$$\left(\frac{810}{810+845}\right)^2 = 0.24$$

(b) turkey vultures supplant black vultures

$$\left(\frac{810}{810+845}\right)\left(\frac{810}{810+845}\right) = 0.25$$

(c) black vultures supplant black vultures

$$\left(\frac{845}{810+845}\right)^2 = 0.26$$

(d) black vultures supplant turkey vultures

$$\left(\frac{845}{810+845}\right)\left(\frac{810}{810+845}\right) = 0.25$$

Multiplying these probability values times 433, the total number of peck/jump patterns

observed, provided expected values for each dyad of classes. Observed frequencies followed by expected values are listed for the following contexts: turkey vultures supplant turkey vultures, 134, 104; turkey vultures supplant black vultures, 130, 108; black vultures supplant black vultures, 151, 113; and black vultures supplant turkey vultures 18, 108. Differences are significant (X^2=100.91, *df*=3, *p*<0.001) with the largest deviation, a negative one, in the class with black vultures supplanting turkey vultures.

Similarly, I compared expected and observed values for the frequency of contested fights among members of these two species. In this analysis the total number of vulture minutes recorded was 3,045 min for turkey vultures and 3,595 min for black vultures. Observed frequencies are listed first, followed by expected values for the following contexts: turkey vulture within-class fights, 22, 7.2; black vulture within-class fights, 12, 9.9; and turkey vulture-black vulture fights, 0, 16.9. Again differences are significant (X^2=47.77, *df*=2, *p*<0.001) with the largest deviation represented by the absence of across-species fights.

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